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BEHAVIORAL ECOLOGY OF COLUMBIAN GROUND SQUIRRELS

by

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Date... March 11, 1982.....

Abstract

The importance of dominance relationships for individual fitness and population ecology of Columbian ground squirrels (*Spermophilus columbianus*) was investigated at an isolated colony in southwestern Alberta from April 1979 to April 1981. All squirrels were trapped and marked, so that they were individually recognizeable. This enabled me to follow them in space and time.

The population was characterized by higher density and litter size than previously reported for this species at this latitude, suggesting that competition for any limited resources was likely to be intense. Yet, squirrels grew rapidly and achieved a prehibernation weight that was greater than that of squirrels from nearby populations, suggesting that food was not limited.

Dominance relationships were determined mainly from observation of agonistic interactions. Adult females became aggressive following breeding, establishing territories within which they were dominant over trespassers of the same sex-age class. Dominance status among females appeared to determine priority of access to optimal territorial sites; adult females that appeared to be forced into habitat judged to be suboptimal raised fewer young and may have been exposed to a greater risk of overwinter mortality, although such mortality was low throughout this study. Levels of aggressiveness among adult females decreased near the time of parturition, coinciding with the lowest level of

trespassing of territories, rose again to peak during lactation, when scent-marking behavior by adult females was also highest, and subsequently decreased after the juveniles emerged. With the decline in aggressiveness following juvenile emergence, territorial defense also subsided, suggesting that protection of infants in burrows may have been the main selective advantage of female territoriality.

Adult female aggressiveness was also directed towards yearlings, particularly males. Most yearlings, regardless of sex, disappeared at the time adult females were most aggressive (during lactation). Adult males also were aggressive towards yearlings, but mainly during the first part of the season. A greater proportion of yearling males than females disappeared, and most were thought to have emigrated; a few yearling immigrants settled in the study area, and two emigrants from this colony were retrapped at other colonies. The number of emigrants greatly exceeded that of immigrants.

Yearling females of this species in southwestern Alberta were previously thought to be sexually immature. However, four raised young in 1980 in the study area, possibly enabled to do so by a combination of good habitat quality and favourable weather conditions. They did not leave the meadow and their social behavior was similar to that of adult females. Yearling emigration was proportionally greater in the year when density was greater. During this study, emigration appeared to be the most

important cause of loss of squirrels from the colony, and predators had little impact on population dynamics; only juveniles were recorded as prey. It is suggested that socially-induced emigration is important in population regulation, and that social status of each squirrel may affect its fitness. By being dominant, a given squirrel could monopolize optimal habitat; in so doing it could evict other squirrels and hence limit population size as well as assuring itself an opportunity to maximize its own reproductive output.

Acknowledgements

This study was made possible by the initiative, advice and encouragement of Dr. David A. Boag. He offered me the chance to start this project before I completed my undergraduate degree, suggested the choice of Dyson Creek as a study area and helped with the fieldwork. Dyson Creek was not only harbouring an interesting population of ground squirrels, but was also a beautiful place to spend time in.

I am very grateful to Dr. Jan O. Murie for stimulating my interest in ground squirrels and providing the observation stand and essential advice and critical input during the planning and execution of the research and the writing of this thesis. Wendy J. King allowed me to use data she collected at Dyson Creek in the summer of 1981, and reviewed and criticized several drafts of the thesis. Valuable advice was also provided by Dr. Linda Fedigan.

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1. Introduction

In recent years, students of animal ecology have become increasingly aware that social behavior plays an important role in population dynamics. Individuals, even of the same sex-age class and from the same population, do not all behave identically (Bekoff 1977). Differences in behavior, particularly social behavior, may have a profound influence on individual fitness as measured by survival and subsequent reproductive output. The study of differential reproductive success is possibly the focal point where behavior and ecology converge. Such studies try to understand population processes by looking at the fates of individuals rather than at groups of individuals and hence of 'average' animals. Almost invariably, a deeper understanding of population ecology is achieved when investigators examine the behavior of individuals rather than considering population parameters alone. This has been demonstrated consistently, and seems to matter little whether the animals studied are aphids (Whitham 1979, 1980) or elephant seals (LeBoeuf 1974; Reiter *et al.* 1981).

Several aspects of the behavioral ecology of some species of nearctic ground-dwelling sciurids have been investigated. Carl (1971) suggested that differential mortality among *Spermophilus parryii* was related to dominance status, but did not present any data on social interactions to substantiate his suggestion. McLean (1981) examined the social behavior of this species, and found that

it affected individual fitness: genetically related females apparently increased their inclusive fitness by behaving altruistically in response to adult males that attempted to kill other male's offspring. The role of kin selection and the effects of altruistic and selfish behavior have been investigated by Sherman (1980, 1981b) for *S. beldingi*. Dunford (1977a, b) suggested that social behavior was important in population dynamics of *S. tereticaudus*, but that it was not effective in stabilizing population size under conditions of low predation pressure and no apparent food shortage. Andersen *et al.* (1976) reported that social status was important in determining access to adequate hibernacula for *Marmota flaviventris*. For this same species, Armitage (1975) developed a model that proposed a means of regulating colony (i.e. population) size through the social behavior of its members. The model stressed the importance of individual variations in social behavior; if highly aggressive animals existed within a low-density colony, interaction rates could be higher than those observed in a high-density colony of less aggressive marmots (Armitage 1975). Thus, the effect of density depended on the nature of individuals in the colony. This appeared consistent with field observations that revealed the lack of any consistent relationship between population density and aggressive behavior in different colonies (Armitage 1975, 1977). Barash (1974b) compared the social organization of different species of marmots, and suggested that social behavior was

responsible for regulation of population size, particularly in those species living in harsh and unpredictable environments. He felt that high population densities led to increased social pressure which caused rates of emigration to exceed immigration among immatures. Armitage (1981) reviewed the extent to which 18 species of burrowing sciurids manifested social behavior. He postulated that sociality was an adaptation to unfavorable environmental conditions, and that it was important in the regulation of populations living under such conditions.

Columbian ground squirrels (*S. columbianus*) have many attributes that make them well suited for a study of behavioral ecology. They live in colonies and interact frequently (Steiner 1970b). They are often found in open habitats where they can be easily observed, habituate readily to the presence of an observer and can easily be trapped and retrapped. They have a long lifespan (Boag and Murie 1981a), so that the same animals can be observed over several years, and age-specific differences in behavior and changes in social status can be documented (Murie and Harris 1978). *S. columbianus* is found in mountainous environments with unpredictable climate. Under these conditions, a high degree of sociality is predicted, which should be important in regulating population size (Barash 1974b; Armitage 1981). However, these rodents also have a number of characteristics, shared with most members of their genus, that make studies of their behavior difficult, the most

important one being their fossorial habits. A Columbian ground squirrel spends most of its life underground, where it is hidden from the observer. Information on social behavior within burrows is completely lacking. A basic assumption in most studies of ground-dwelling sciurids is that behavior observed while the animals are above ground is not affected by that occurring underground. In addition, information on paternity and male reproductive success is largely lacking because copulations apparently occur in burrows. Also, the fate of individuals that disappear from the study area is almost always unknown, making it difficult to distinguish mortality from emigration.

In southwestern Alberta, this squirrel occurs in colonies of varying size. Previous researchers have pointed out the desireability of studying a small, isolated colony, so that all members of the population could be marked and followed individually (Balfour 1979; Boag and Murie 1981b). Observing an entire colony also eliminates the problem of peripheral animals, part of the same biological population but living mainly outside the boundaries of the study area, yet interacting with the study animals in unclear contexts.

Aspects of the life history of *S. columbianus* have been investigated by Shaw (1924, 1925a,b, 1926, 1945), Manville (1959), Michener (1977), and Boag and Murie (1981a). Its behavior has been described by Steiner (1970a,b, 1971, 1972, 1973, 1974) and Betts (1973, 1976). Murie and Harris (1978) examined the spacing system of males in spring, and found

that dominant adults were territorial during the breeding season. They suggested that dominant males perform most of the breeding. Available information on the population ecology of this species is limited to natality rates (Murie *et al.* 1980) and information obtained through long-term trapping of a large population (600+ squirrels) (Boag and Murie 1981b).

In late April 1979 I started a study of the influence of some aspects of social behavior on the population ecology of Columbian ground squirrels in an isolated colony in southwestern Alberta. This research addressed five major questions:

1. Does behavioral dominance exist among *S. columbianus*?
   Murie and Harris (1978) had shown it to exist among adult males, but little was known about other 'sex-age' classes.
2. How is dominance established and maintained, and what factors are important in this process?
   Murie and Harris (1978) reported that both age and location (relative to an animal's core area) were important in maintaining dominance status among resident males, based on the outcome of aggressive interactions.
3. What (if any) advantages are enjoyed by dominant squirrels?
   Wilson (1975) listed several possible advantages of being dominant. Access to estrous females seemed to be a prerogative of dominant male *S. columbianus* (Murie and

Harris 1978), but no comparable information was available for females or immatures.

4. What alternative strategies are adopted by subordinates? This is a very important question that is often overlooked. Only recently has attention been paid to the means by which animals minimize the disadvantages caused by a subordinate status (Wilson 1975; Whitham 1980; Reiter *et al.* 1981).
5. Is social behavior important in population dynamics, and does it play a significant role in population regulation?

   Boag and Murie (1981b) found that within a large colony, Columbian ground squirrels were not evenly dispersed. Clumps of high population density existed. Residents of these clumps appeared to enjoy higher survival, and immigration to these clumps was less than emigration from them. They hypothesized that subordinate animals were excluded from these clumps (supposedly located over optimal habitat) through some behavioral mechanism.

The results of this study are presented in four chapters, each being a self-contained unit except for the description of the study area and the general procedures followed in collecting data, outlined in a separate section on 'Study Area And Methods'. Body-weight data, additional to those presented in the chapter on yearling female reproduction, are summarized in Appendix 1. An overall discussion concludes this presentation with consideration of

population regulation and speculation regarding the process of colonization of new habitat by *S. columbianus*.

2. Description Of Study Area And Methods

The study area (Fig. 1), located in the foothills of southwestern Alberta within the Sheep River drainage, approximately 32 Km west of Turner Valley, Alberta, consists of a small isolated grassy meadow (elevation 1570 m) surrounded by mixedwood forest of poplar (*Populus*) spp. and lodgepole pine (*Pinus contorta*). The meadow is dominated by *Poa pratensis* and *Phleum pratense*, with a few clumps of *Potentilla fruticosa* and *Ribes oxycanthoides* and a few isolated aspen (*Populus tremuloides*). Other important grasses and herbs include *Agropyron smithii*, *Stipa columbiana*, *Muhlenbergia asperifolia*, and *Achillea millefolium*. Several boulders and rocks are scattered over the meadow. A permanent stream, Dyson Creek, divides the study area in two sections; a northern section, henceforth referred to as SA (0.74 ha), was observed intensively, while the southern section, henceforth referred to as SSD (approximately 0.30 ha), was not. Behavioral data were collected from squirrels in SA only, but demographic data also include those found in SSD. The squirrels could easily ford Dyson Creek when it was not in flood, but they seldom did so and very few lived in SSD. Each year only one adult female and her litter plus a few yearlings (2-4) spent most of their time in this section.

A single-track dirt road, closed to all but forestry traffic, crosses the meadow and allows vehicular access after snowmelt. When snow prevents this, a hike of about 50

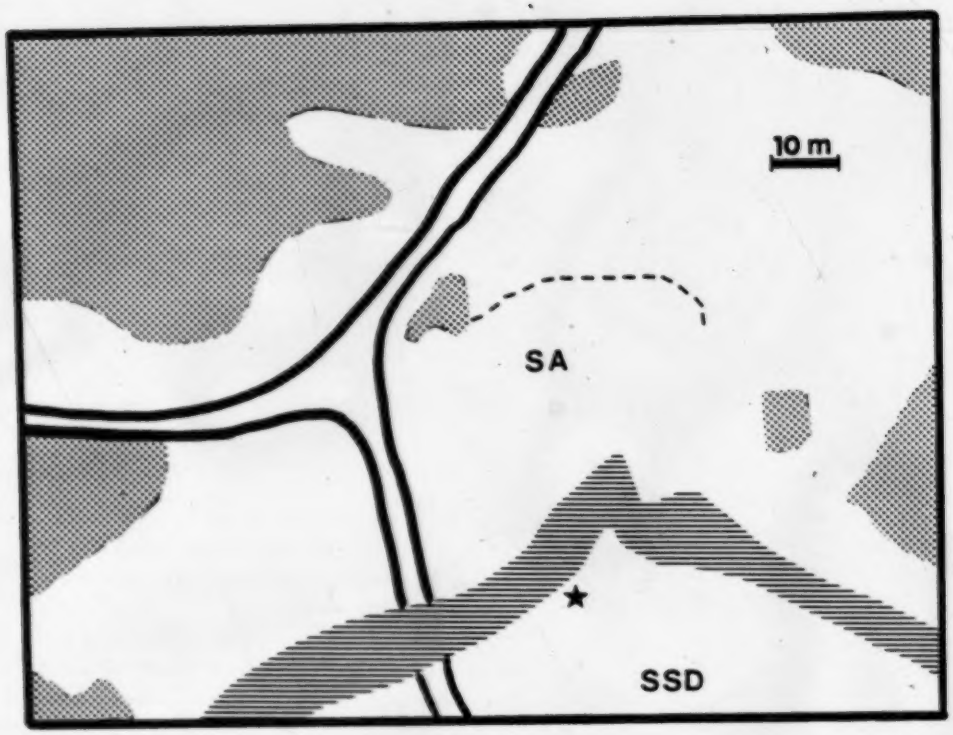


Fig. 1. Map of Dyson Creek study area. Stipled areas show location of forest and hatched strip, the location of Dyson Creek. Solid lines indicate roads, and broken line the top of a steep ridge, approximately 2 m high. The star indicates the location of the observation stand in the small meadow on the south side of the creek (SSD).

minutes is necessary to reach the study area. The meadow was the site of a sawmill, the remains of which were removed in 1965. Consequently the vegetation present in the lower flat areas, near the creek, grows on soil that has a large component of sawdust in it. A steep ridge, approximately 2 m high, surrounds these flat areas, and from the top of this ridge the meadow slopes upward to the surrounding forest with increasing steepness.

Cattle graze the meadow from July through September. This permitted behavioral observations throughout the entire summer, as grazing prevented grasses from growing to an height that would have hidden the squirrels.

The closest colony of Columbian ground squirrels (about 25 animals) is approximately 2 km to the west. Several small colonies exist in meadows farther west, while large colonies (300+ squirrels) are located approximately 3 km north and 4 km south. The colony 2 km to the west (Rosengroen) was trapped in 1979 and 1980, but not all residents were captured in 1979. The entire population at this site was marked in 1980. The large colony to the north (Gorge Creek) had been trapped from 1973 to 1979 (Boag and Murie 1981a,b) and up to 1979 most squirrels were marked. In 1980, only a small portion of the Gorge Creek area was trapped.

Work started at Dyson Creek on 25 April 1979, 1 day before the first squirrel emerged that year. A 10-m grid was laid over SA, and small (10X10 cm) plastic flags on wire stakes were placed at all grid intersection points. The

coordinates of each flag were written on it with a grease pencil. Locations of squirrels were recorded by visually estimating the distance they were from the lower left hand corner flag (on the X and Y axis) of the grid square in which they were observed. I have no estimate of error for these locations, but I believe that most were accurate to within 1 m, and it is unlikely that any were more than 2 m off.

Ground squirrels were trapped with National Live Traps (15 X 15 X 50 cm) baited with peanut butter and placed at burrow openings. A numbered fingerling fish tag (National Band and Tag Co. Monel No.1) was clipped on each ear for permanent identification. To make them identifiable during observations, squirrels were either dyed with commercial hair dye (Lady Clairol Nice'n Easy natural blue-black, #124) or marked with a small colored plastic flag (Saflag Co.). This flag was either sown through the ear or slipped under the metal tag, bent over and stapled closed. Different color combinations (one flag per ear) were used for each squirrel. With the exception of one juvenile each year, the entire population was captured, tagged, and individually recognizeable. When the marks on hair-dyed squirrels became unrecognizeable (at molting) they were recaptured, usually within a few days, and remarked. Individuals known to be difficult to trap were marked with plastic ear flags whenever possible to avoid the necessity of retrapping.

After the initial intensive trapping in spring 1979, SA was trapped every 4-5 days with 20-30 traps, whereas SSD was trapped about once every 2 weeks. Trapping was more intensive when molting occurred and juveniles emerged. Burrows from which juveniles emerged were surrounded with 4-6 open traps, usually as soon as a new litter was noticed. This prevented the juveniles from going anywhere but into a trap when they walked away from the burrow. In 1980, 9 juveniles were hand-caught by ambush at burrow openings. At each capture, squirrels were weighed and their tags and markings checked. Dyemarks were redone whenever they began to fade. Reproductive status was also noted. Females were checked for swelling and opening of the vulva during the breeding season, and swelling of the nipples during lactation. Males were checked for scrotal pigmentation.

Ages of squirrels were known with certainty for all those born in 1979 or 1980. Untagged squirrels caught in the spring of 1979 were classified by weight as either yearlings or adults (Boag and Murie 1981a).

Family relationships were determined by tagging entire litters at their emergence burrows or their immediate vicinity and confirmed later through observations of dispersion during the first 2-3 days following emergence. In 1979 this was facilitated by the wide spacing between emergence burrows and the temporal spacing of emergences, but in 1980 two litters on the ridge in the middle of SA emerged on the same day and very close to one another. The

family relationships of one juvenile male belonging to one of these two litters could not be determined.

Observations were conducted from the ground in SSD (Fig.1) until mid-June 1979, and from a 2-m high wooden stand thereafter. The study area was observed with 10X50 Zeiss binoculars and the identity, location, and activity of squirrels were noted. All social interactions seen were recorded, including identity of interactors, location and type of interaction, and its outcome, that is which squirrel (if any) lost or won the interaction. For chases, both the location where it started and ended (the location where the chaser stopped, a fight broke out, or a chase reversal occurred) were recorded whenever possible.

Approximately one third of the observation time was spent recording social interactions only, including chases, fights, threats, 'play', and 'greeting' (Steiner 1970b). Otherwise SA was scanned from end to end and only the first sighting of each squirrel for each scan was recorded, unless the same animal was later seen involved in an interaction before the scan was completed. Due to the large number of squirrels, scans lasted up to 20-25 minutes each, and no attempt was made to perform them at regular time intervals.

In 1979, observations were conducted from 28 April (2 days after emergence of the first squirrel) to 21 August (one day before the last two squirrels immerged), for 245 hours on 106 days. In 1980, 196 hours on 96 days were spent observing between 24 April, when 21 squirrels had already

emerged (although none was seen on 18 April) and 13 August, when the last squirrel disappeared. In 1981 I trapped the study area from 17 to 22 April, but I made no behavioral observations.

Most observations were made between 0730 and 1100 MDT, but ranged from 0700 to 2030 at various times during the study. Observations were not conducted when adverse weather conditions (rain, heavy snow or hot temperatures) reduced the activity of squirrels, so that only a few were active above ground at any one time. In 1980, juveniles were not observed intensively. They were individually recognizeable, but their location and activity were recorded only when they interacted with a non-juvenile squirrel.

Each year the season was divided into 11 8-day periods and a 12th Period that lasted until immergence of the last adult female. Period 1 started each year on the first day of observations. Periods 1-2 generally included the breeding season, Periods 2-4 gestation, and Periods 4-7 lactation. Most juveniles emerged during Periods 7 and 8, and most squirrels entered hibernation during Period 12. Only a few juveniles each year were still active for a few days after the end of Period 12, which was on 13 August in 1979 and on 11 August in 1980. However, the population was not synchronized in its yearly cycle, particularly in 1979. For example, each year some females emerged after others had already bred, and consequently their litters also emerged later.

Individual rates of behavior were calculated by dividing the total number of behavioral acts observed by the number of observation hours during which a given squirrel was active in SA. Time spent watching during days in which that squirrel was not sighted, or was seen in SSD only, were not included in this calculation. The manner by which these data were analyzed is given in the specific chapters.

3. Dispersal In Columbian Ground Squirrels

3.1 Introduction

Several hypotheses have been put forward to explain the ecological significance of dispersal in sciurids, including avoidance of inbreeding and competition for mates (Dobson 1979). Many studies also suggest that dispersal may play a role in population regulation (Armitage and Downhower 1974; Slade and Balph 1974; Dunford 1977a; Michener and Michener 1977; Boag and Murie 1981b).

However, even though it is generally accepted that dispersal occurs regularly and that it is an important population attribute, little is known about its proximate cause(s). As Anderson (1980) pointed out, most studies have approached this problem from the point of view of the dispersing animals. In so doing, they have tried to identify advantages of dispersal that may make it attractive to the individual, without considering the possible coercive effects of members of the population such as the older, dominant residents. This possibility becomes particularly important under conditions of high population density, when resident adults may be more motivated to avoid competition, in extreme cases even with their own offspring (Anderson 1980). In fact, high-density populations are often characterized by rates of emigration that are high relative to immigration (Slade and Balph 1974; Dunford 1977a). Even

so, often not all members of the potentially dispersing sex-age class(es) actually disperse.

Another aspect of dispersal that has received little attention is the behavioral ontogeny of dispersers and non-dispersers while both groups are still resident within their natal population. Little is known about either the social behavior of those individuals that do not disperse or the means by which they are recruited into the population. Bekoff (1977) stressed the need for more information on these aspects, pointing out the high degree of variability that exists in social behavior among individuals, and suggested that a detailed knowledge of individual life histories was needed to understand the process of dispersal. He also suggested that a high degree of individual variability was a possible explanation for the often unclear or non-existent relationship between dispersal and aggressiveness or dominance. A similar argument was presented by Armitage (1975, 1977), to explain the lack of a consistent relationship between density or aggressiveness and dispersal in different colonies of *Marmota flaviventris*.

Dispersal has been studied in several species of ground-dwelling sciurids, including *M. flaviventris* (Armitage 1974; Armitage and Downhower 1974), *M. monax*(Davis *et al.* 1964),*Spermophilus richardsonii* (Michener and Michener 1973, 1977; Schmutz *et al.* 1979), *S. beldingi* (Sherman 1980), *S. beecheyi* (Dobson 1979), *S. tereticaudus* (Dunford 1977a), *S. armatus* (Slade and Balph 1974), and *S.*

parryii (McLean 1981). For all of these species, dispersal occurs mainly or solely among young animals that are usually sexually immature. Young males are always more likely to disperse than young females. This trend has been reported also for *S. columbianus* (Betts 1973; Boag and Murie 1981b).

I present here data on emigration and immigration at the Dyson Creek study area, with an emphasis on social behavior between adult residents and yearlings.

3.2 Methods

Behavioral data were collected following the procedures outlined in the section on methods. Data from the four yearling females that raised litters in 1980 were not included in this analysis, because of their peculiar behavior with both yearling and adult characteristics (Chapter 4).

All rates presented in this chapter are per unit time per individual squirrel. For each individual, only the time spent observing during days in which it was sighted aboveground in SA was used in calculating these rates and the expected numbers of interactions to be compared with those actually observed. For example, suppose that the total number of interactions for two sex-age classes (A and B) was 100. If the cumulative observation time of class A was 80 hours (e.g. 4 animals for 20 hours each) and that of class B was 20 hours (e.g. 1 animal for 15 hours and another for 5

hours), I would expect, if interactions occurred at random, class A to have 80 and class B 20.

Population data presented in this chapter include squirrels from both SA and SSD.

3.3 Results

The population studied at Dyson Creek is described in Table 1. Included are squirrels that were resident in the area when this study began as well as those recruited through both natality and immigration. The figure for juveniles at emergence indicates the number emerging from the natal burrows in late June. Squirrels were classed as yearlings after their first winter.

Overwinter survival among all sex-age classes was high in both years (Table 1): over 80% of squirrels entering hibernation emerged again the following spring. If juveniles born in 1980 are excluded, this figure rises to over 90%. Survival during the active season was higher in 1979 than 1980 (chi-square = 6.71, one degree of freedom, $P<0.01$). In both years yearlings showed a greater reduction in numbers during the summer than either adults or juveniles. Among yearlings, more males disappeared than females. This difference, however, is not significant for the 2 years combined (chi-square = 3.72, $0.1>P>0.05$), unless the four breeding yearling females of 1980 (Chapter 4) are included (chi-square = 7.8, $P<0.01$). Almost all yearling

Table 1. Composition and survival of the population of Columbian ground squirrels at Dyson Creek from 1979 to 1981.

Year	Adults				Yearlings				Juveniles			
	♂♂	♀♀	Σ	Sx(%)[a]	♂♂	♀♀	Σ	Sx(%)	♂♂	♀♀	Σ	Sx(%)
1979												
Emergence	2	10	12	100	7	7	14	57	26	15	41	90
Immergence	2	10	12		3	5	8		23	14	37	
1980				92				100				97
Emergence	2(5)[b]	9(14)	11(19)		23	13	36		26	24	51[c]	
Immergence	1(2)	8(11)	9(13)	68	4	7	11	31	17	15	32	63
1981												
Emergence	2(5)	11(18)	13(23)	100	15	12	27	91				84

[a] Survival of both sexes combined.

[b] Numbers in brackets include surviving adults plus newly recruited yearlings from previous year.

[c] Includes one juvenile of unknown sex.

disappearances from the study area occurred within a relatively short and well-defined period (Table 2) and are believed to represent dispersal.

The 1979 juvenile cohort was followed until its third summer during this study (Fig. 2); the major loss of individuals for both sexes occurred during the summer of 1980 when these squirrels were yearlings.

Adult squirrels of both sexes were aggressive towards yearlings (Figs. 3 and 4). Adult female aggressiveness reached a peak during Periods 6-7, coinciding with late lactation and emergence of juvenile squirrels from the natal burrows (mid- to late June). Most yearlings disappeared during Periods 6 to 8 (Table 2). Yearling males tended to leave earlier than yearling females. The rate of aggressive behaviors of adult females towards yearlings was higher in 1980 than in 1979 (Wilcoxon signed-rank test, $P<0.005$ for all periods and also for Periods 1-9 only). Aggressiveness of adult males towards yearlings was higher in 1979 (Wilcoxon signed-rank test, $P<0.025$ for Periods 1-12 and $P<0.05$ for Periods 1-9). With the exception of adult males in 1980, adults of both sexes chased yearling males more frequently and yearling females less frequently than would be expected if chases were at random with respect to sex (Table 3).

In 1979, those yearlings that subsequently emigrated were chased much more often than non-emigrants (Table 3). This difference was not as great in 1980, when all yearlings

Table 2. Timing of disappearance of yearling Columbian ground squirrels from Dyson Creek in 1979 and 1980.

Year	Sex	N	Median date of disappearance	Range
1979	♂♂	4	June 16	June 11 - 28
	♀♀	2	June 29[a]	June 23 - July 4
1980	♂♂	18	June 18	June 8 - 30
	♀♀	6	June 28	June 16 - July 2

[a] Mean

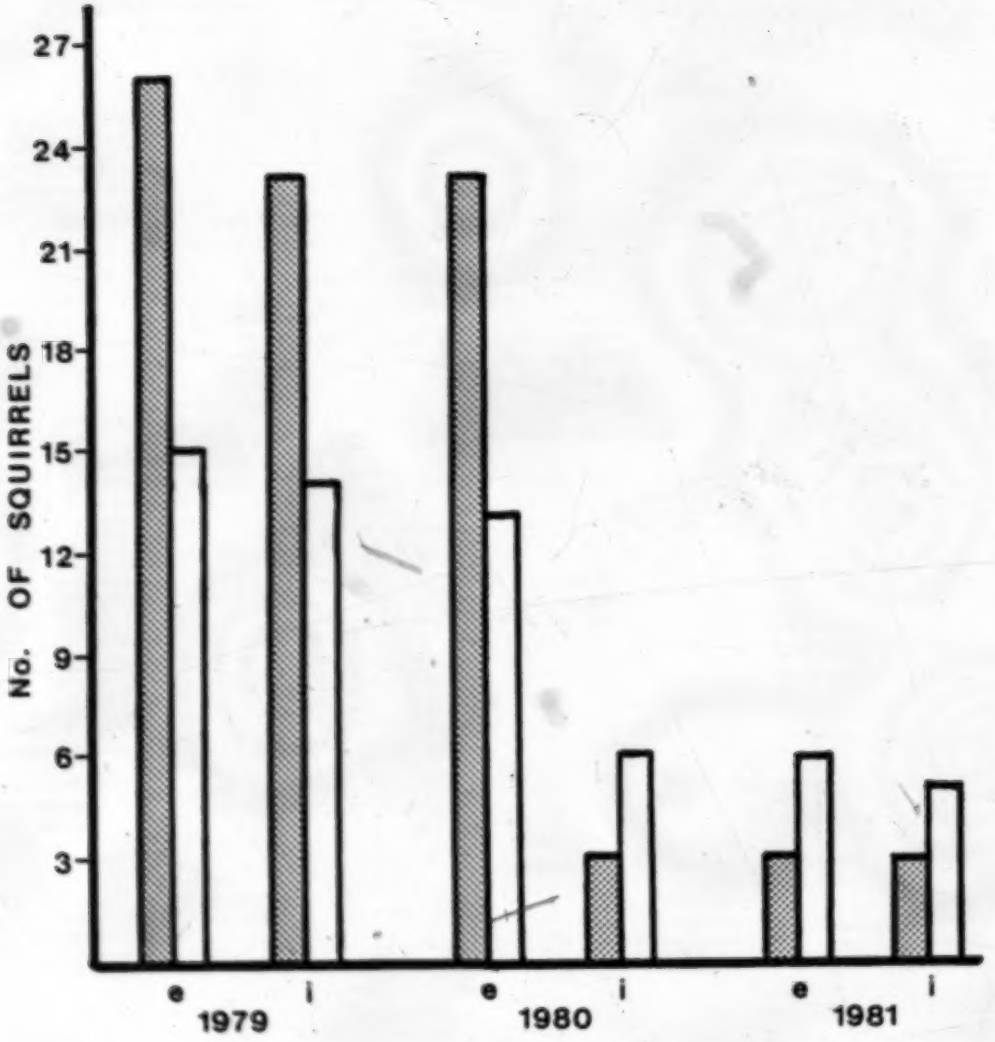


Fig. 2. Residence within natal colony of a cohort of Columbian ground squirrels born at Dyson Creek in 1979. Males are indicated by stipled bars and females by open bars. e = emergence; i = immergence; 1981 immergence data from W.J.King (pers. comm.).

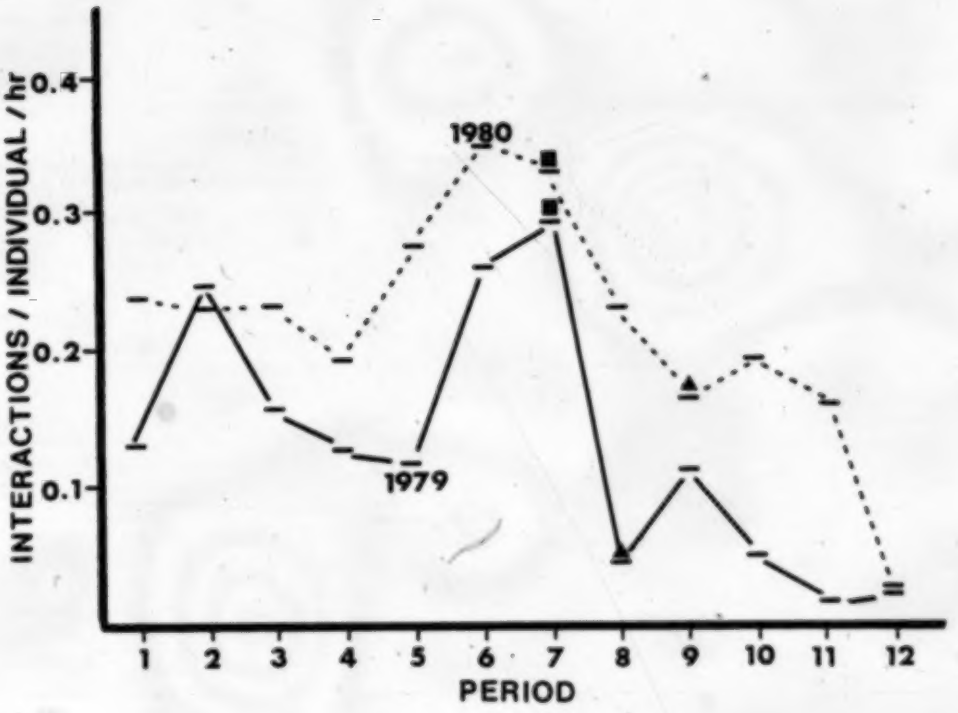


Fig. 3. Rates at which yearling Columbian ground squirrels were being chased by adult females at Dyson Creek in 1979 and 1980. Yearling immigrants in both years and yearling females that bred in 1980 (Chapter 2) were excluded from calculations. Squares indicate the median period of disappearance of yearling males, and triangles the median period of disappearance of females in each year.

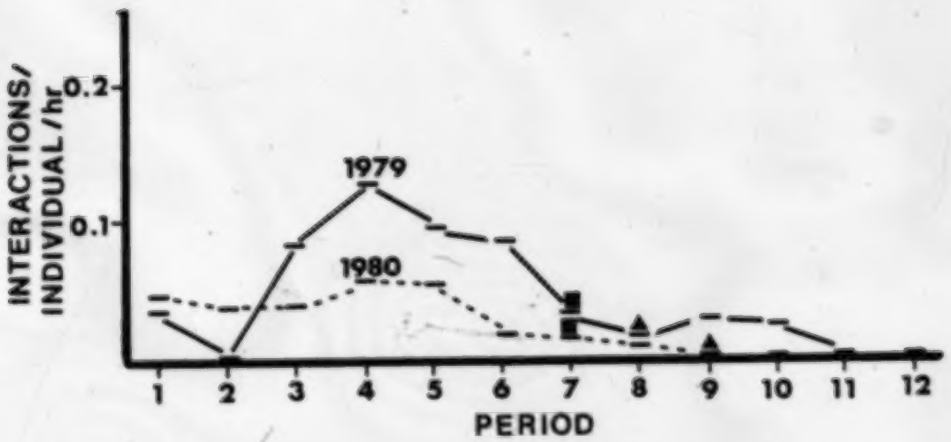


Fig. 4. Rates at which yearling Columbian ground squirrels were being chased by adult males at Dyson Creek in 1979 and 1980. Yearling immigrants in both years and yearling females that bred in 1980 (Chapter 2) were excluded from calculations. Squares indicate the median period of disappearance of yearling males, and triangles the median period of disappearance of females in each year.

Table 3. Comparison of observed and expected numbers of aggressive interactions between adult Columbian ground squirrels and different groups of yearlings at Dyson Creek in 1979 and 1980. Expected values were calculated by dividing the total number of interactions by the cumulative observation time for each two groups compared and multiplying by the cumulative observation time for each group (see text). Only observations before the time of dispersal (Periods 1-9) are considered.

Sex of adult	Yearlings	Year	Observed	Expected	χ^2	Probability
♀	♂♂	1979	129	106.9	7.85	<0.01
	♀♀		127	149.1		
♀	♂♂	1980	584	500.8	43.63	<0.0001
	♀♀		149	232.2		
♀	Emigrants	1979	176	137.5	23.29	<0.0001
	Non-emigrants		80	118.5		
♀	Emigrants	1980	608	586.8	3.84	0.05
	Non-emigrants		125	146.2		
♂	♂♂	1979	52	39.3	7.05	<0.01
	♀♀		42	54.7		
♂	♂♂	1980	61	60.8	0.002	>0.5
	♀♀		28	28.2		
♂	Emigrants	1979	60	50.5	4.26	<0.05
	Non-emigrants		34	43.5		
♂	Emigrants	1980	79	73.1	2.23	>0.1
	Non-emigrants		14	19.9		

were chased more frequently. In both years, aggressive interactions towards yearlings from adult females were more frequent than from adult males.

Records of long-distance movements by dispersing yearlings were few in number (Table 4; see also Boag and Murie 1981b). Recruitment of immigrants to the colony was characterized by high levels of aggressiveness directed at the immigrants by resident squirrels. When an immigrant first entered the colony, adult females chased it; these chases were much longer than those between adult females and resident yearlings. The immigrants were always chased until they either disappeared into the treed areas surrounding the meadow or entered the territory of a neighboring female which in turn chased them. Immigrants eventually established themselves in peripheral areas, away from the resident adult females. Near the end of the season, however, immigrant yearling males became more aggressive and stood their ground when attacked by adult females, often forcing them to retreat. By this time, however, adult females were also much less aggressive (Fig. 3). Non-emigrating yearling residents showed a similar pattern of behavior in 1980. In 1979, a group of four yearlings (one male and three females) lived in one section of SA where adult females were more widely spread than elsewhere. This group of yearlings was chased much less than the other, that lived around the ridge in the center of SA. No yearlings of the former group dispersed but of the latter (four males and three females), only one

Table 4. Dispersal movements of Columbian ground squirrels between three study areas in southwestern Alberta. Distance moved is the straight-line distance between capture points.

Sex	Last capture before dispersal (age)	First capture after dispersal (age)	Distance moved (Km)
♂	Gorge Creek Aug 1/77 (Juv)	Rosengroen June 1/79 (Ad)	4.1
♂	Gorge Creek Jun 10/79 (Y1g)	Dyson Creek July 2/79 (Y1g)	2.9
♂	Gorge Creek May 31/79 (Y1g)	Dyson Creek May 1/80 (2yr)	3.1
♂	Dyson Creek Jun 10/80 (Y1g)	Rosengroen June 12/80 (Y1g)	2.0
♂	Dyson Creek Jun 18/80 (Y1g)	Gorge Creek Jun 30/80 (Y1g)	2.7
♂	Untagged	Dyson Creek Jun 24/80 (Y1g)	?
♀	Untagged	Dyson Creek Jun 24/80 (Y1g)	?

female did not disperse. The changes in the centers of activity of this yearling female over the season of 1979 are plotted in Fig. 5. This squirrel moved to an area used very little by adult females during Periods 8 to 11, and returned to its original home range just before hibernation. In SSD, where only one adult female lived in both years, two of three yearlings (one of each sex) in 1979 and one of three (a male) in 1980 remained until hibernation.

Several of the yearlings that disappeared in 1979 increased their range of movements before leaving; for 5 of 6 presumed to have emigrated the median distances at which they were sighted from their centres of activity increased by more than 100% during the last period before they disappeared.

In 1980, a flat area in the center of SA near the creek was not used by adult females until late in the season, past the peak of aggressiveness. Yearlings assumed to have dispersed clumped in this area before they disappeared (Fig. 6). After they did so, the rate of aggressive behaviors from adult females decreased (Fig. 3), possibly because of fewer chances of an adult female-yearling encounter. Of the five non-breeding yearlings that did not emigrate from SA in 1980, two males moved to the periphery of the study area during Periods 8 through 10, one female moved to SSD, another stayed within the area of low adult female density, and one male disappeared for 12 days, then returned.

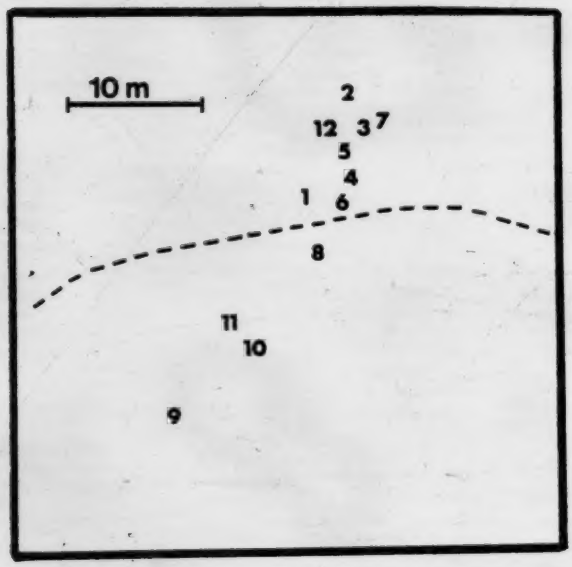


Fig. 5. Centers of activity of a non-emigrating yearling female at Dyson Creek in Periods 1-12 of 1979. Numbers indicate the location of centers of activity for the corresponding periods. Broken line indicates the top of the ridge in the center of SA, where several adult female territories were clustered (Chapters 3 and 4).

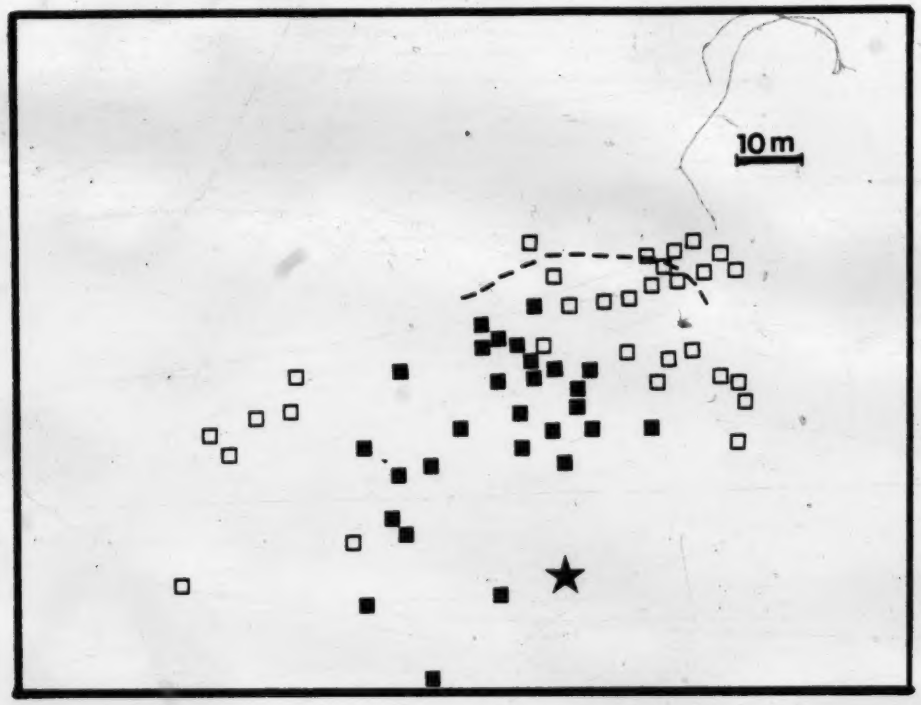


Fig. 6. Centers of activity of yearling Columbian ground squirrels that disappeared at Dyson Creek in 1980. Open squares indicate centers of activity during Period 1, or the first period following emergence. Black squares indicate centers of activity during Period 8, or the last period before disappearance. Broken line indicates the top of the ridge in the center of SA. Star indicates the location of the observation stand.

As shown in Table 5, near the end of the season the three non-emigrating males improved their social status and fought back when attacked. By this time they weighed more (750-770 g) than most adult females (590-780 g). These three squirrels appeared dominant among other members of their sex-age class (Table 6). However, the only significant difference between them and those that disappeared was in the number of aggressive interactions they won as yearlings. Many of the yearling males that disappeared won several aggressive interactions with other yearling males. The only yearling male that did not disappear from SA in 1979 was never seen to interact with another yearling male, and so its dominance status was unclear, however it was often subordinate to yearling females. Fewer aggressive interactions occurred among yearling females, so most dominance relationships remained uncertain. The four that bred in 1980 and did not emigrate were much more aggressive than other members of their sex-age class (Chapter 4). Nevertheless, other non-breeding non-emigrating yearling females gave no evidence of being dominant individuals.

3.4 Discussion

The data presented indicate that most Columbian ground squirrels disappear as yearlings during the time adult females are in late lactation and juveniles are emerging. These yearlings are presumed to have emigrated. This agrees

Table 5. Aggressive interactions between adult female Columbian ground squirrels and three non-dispersing yearling males at Dyson Creek in 1980. Numbers in brackets indicate interactions seen for each yearling male every 10 hours of observation.

Outcome	Aggressive interactions[a]	
	Periods 1-9[b]	Periods 10-12[c]
Adult female dominant	98 (2.48)	12 (0.75)
Yearling male dominant	1 (0.03)	9 (0.56)

[a] difference in frequency of outcomes between the two groups of Periods, $\chi^2 = 35.41$ with 1 degree of freedom, $P<0.0001$

[b] 131.6 hours of observation

[c] 53.5 hours of observation

Table 6. Outcome of agonistic interactions between male Columbian ground squirrels born at Dyson Creek in 1979. Ranges are given in parentheses. Only interactions occurring before the time of dispersal are included for yearlings.

Year (age)	Presumed emigrants (N=18)			Non-emigrants (N=3)		
	wins	losses	ratio $\frac{W}{L}$	wins	losses	ratio $\frac{W}{L}$
1979 (Juv)	1.39 (0-3)	2.28 (0-5)	0.61	6.67 (1-15)	1 (0-3)	6.67
1980 (Y1g)	3.61 (1-11)	5.89 (0-13)	0.61	15.33* (7-29)	3.33 (1-7)	4.60

* $P<0.05$, Mann-Whitney U test comparing interactions won as yearlings by presumed emigrants and non-emigrants

with the findings of Betts(1973) and Boag and Murie (1981b). Almost all juveniles remained on the study area until hibernation in 1979, but in 1980 several disappeared during their first summer. These disappearances, however, were more likely due to mortality than to emigration. Although juveniles are known to disperse in several species of this genus (Michener and Michener 1973; Slade and Balph 1974; Dunford 1977a; Dobson 1979; McLean 1981), neither this study nor those of Betts (1973) and Boag and Murie (1981b) found any evidence of juvenile dispersal in *S. columbianus*. At Dyson Creek, juveniles spent only about 45-50 days above ground during their first summer, within which they had to accumulate sufficient fat for hibernation. Juveniles enter hibernation weighing much less than adults (Boag and Murie 1981a; see also Appendix 1). It may therefore be disadvantageous for them to use some of this time for a long-distance movement, which likely requires a large energy expenditure. The social stress connected with entering a new colony is also likely to be energetically demanding, and a small-bodied juvenile may be at a great disadvantage in the face of aggression from residents. Among *S. parryii*, in which juvenile dispersal does occur, weight of juveniles at immergence is about 90% of that of adults, and the active season of juveniles is over 80 days for females and over 100 days for males (McLean 1981). In addition, juveniles at Dyson Creek were tolerated by adult members of the population. Those instances of aggressiveness that were seen

usually terminated when a juvenile assumed a submissive posture (Steiner 1970b). Tolerance of juveniles by adults has been reported also in those marmot species that delay dispersal to their second summer (Armitage and Downhower 1974), whereas aggression towards juveniles occurs in *S. parryii* (Steiner 1972; McLean 1981) and *S. beldingi* (Sherman 1980, 1981a) that disperse as juveniles.

Boag and Murie (1981b) suggested that some 2-year old males may also disperse. At Dyson Creek, the only yearling male that did not emigrate from SA in 1979 disappeared in 1980 as a 2-year old, at the same time yearling males were disappearing that year (June 16). This squirrel was very small (280 g at emergence, cf. Boag and Murie 1981a) and exhibited behavior patterns (such as play) that resembled those of yearlings more than other 2-year olds, none of which emigrated.

One characteristic of the Dyson Creek study area that may have affected emigration was its location, being surrounded by unfavorable habitat. This may have deterred emigration, thus partially explaining the very high density of squirrels at this site (see Chapter 5).

Aggressive behavior of adults, particularly females, appeared to be involved in stimulating, if not forcing, emigration of yearlings. The latter disappeared when adult female aggressiveness was at its peak (see also Chapter 5). In addition, more male than female yearlings emigrated, and it was this sex-age class that was chased most intensively.

In 1979, assumed emigrants were chased by adult females much more often than non-emigrants. Adult males also chased preferentially the groups of yearlings that apparently emigrated, but each yearling was chased by a male less frequently than by a female. In addition, the peak in adult male aggressiveness occurred early in the season, overlapping with the breeding period, when males are generally more aggressive (Murie and Harris 1978). At the time of dispersal, adult male aggressiveness was low. Dunford (1977a) found that the aggressiveness of resident adults was involved in emigration of juvenile *S. tereticaudus*, but believed that aggressive behavior alone was not sufficient to induce emigration. A similar opinion was expressed by Armitage (1974) for *M. flaviventris*. Aggressiveness towards the dispersing age class has been reported also in *M. flaviventris* (Armitage and Downhower 1974), and suspected to influence emigration in several species of ground squirrels (Steiner 1972; Michener and Michener 1973; Slade and Balph 1974; Boag and Murie 1981b). However Dobson (1979) found no evidence that residents were aggressive towards juveniles that subsequently emigrated in *S. beecheyi*. It is unlikely that the aggressiveness of adult females was directly responsible for emigration in yearling *S. columbianus* because, even at peak frequency of aggressive interactions, each yearling was seen to be chased less than once every 2 hours. No fights resulted in visible wounds and aggressive behavior of adult females did not seem to

interfere significantly with the feeding activity of yearlings. However, such interactions may serve to indicate the conditions of high density present in the study area. This may have stimulated yearlings to search for an area with lower density and possibly a better chance of reproduction. The wider movements in 1979 and the move to the central flat area in 1980 (Fig. 6) may have represented an attempt to avoid aggression without leaving the meadow.

Anderson (1980) pointed out possible advantages that adult females would enjoy by inducing emigration in young animals. In an high-density population such as the one at Dyson Creek, an adult female may benefit from the dispersal of yearlings in several ways. Competition would be reduced, both for herself and for her offspring. Competition is unlikely to be for food, which, based on weight characteristics of this population (Appendix 1), never appeared to be a limiting factor. However, other resources may potentially be limited, such as access to hibernacula and preferred sites within the meadow (Chapter 6). Presence of a smaller number of yearlings may reduce social harassment of juveniles, that were occasionally chased by the few non-emigrating yearlings. If females gained advantage from emigration of yearlings, one could predict that they would be more aggressive towards them when density was higher, because a greater density represents a greater potential competition. This prediction is supported by the data for 1980, when the density was greater and yearlings

were chased more often than in 1979; since the number of adult females that reared litters on SA increased only from 9 in 1979 to 10 in 1980 (Chapter 5), it is unlikely that the larger number of chases shown in Fig. 3 was due to a larger number of females being present.

Adult females may be more aggressive towards male than towards female yearlings because the former may present a greater potential threat to the juveniles, either through direct aggression or through competition for hibernacula or other limited resources found within the adult female's territory (Chapter 5). Yearling males that did not disperse in 1980 were dominant to adult females near the end of the season, and presumably able to displace them from preferred hibernacula.

Adult males would gain advantage by expelling yearling males to avoid competition for mates. They would benefit less from expelling females, that are potential mates (Anderson 1980). Adult males were in fact more aggressive towards yearling males, but in neither year did they show a very strong preference for chasing yearling males over yearling females. In 1980, they seemed to chase yearlings at random with respect to sex. However, four yearling females reared litters in 1980 (Chapter 4), and it is possible that others may have shown some sexual development which could have attracted adult males. Therefore, many of the adult male-yearling female interactions may have been sexual rather than aggressive. Males regularly chase adult females

during the breeding season (Murie and Harris 1978).

Adult females were very aggressive towards immigrant yearlings. This is a common behavior among burrowing sciurids, and is often thought to prevent or limit immigration (Michener and Michener 1973; Armitage and Downhower 1974; Dunford 1977a; Dobson 1979). Aggressiveness could be motivated by protection of juveniles. "Strange" squirrels are responsible for most intraspecific infanticide in *S. beldingi* (Sherman 1980, 1981a) and *S. parryii* (McLean 1981). However, despite being attacked by residents, all immigrants recorded in this study remained on the study area, although possibly other immigrants were present for only a few hours or a day, and went unnoticed. Since it may have been particularly stressful to attempt another dispersal movement, immigrants may avoid the aggressive residents and remain at the periphery of the colony despite the already high density.

Aggressive behavior among squirrels probably influenced dispersal, but the role of dominance status of yearlings in this movement remains unclear. Bekoff (1977), reviewing dispersal in mammals pointed out how both very dominant and very subordinate individuals may disperse, depending on their previous history. Slade and Balph (1974) suggested that dispersal may be advantageous for subordinate individuals that would have had little chance of reproduction had they remained within a high-density population. However, as Anderson (1980) remarked, dominance

relationships among the members of the dispersing class may not determine which individual does and does not disperse if the main driving force of emigration is aggression from older residents that are dominant to all. This factor was very important for the Dyson Creek population. The three yearling males that did not disperse in 1980 were dominant, but other high-ranking yearling males dispersed in the same year, and the only non-emigrant male of 1979 was apparently a subordinate, that possibly dispersed the following year. Among females, the four breeding yearlings of 1980 were more aggressive than other yearling females after becoming pregnant, but their social status was influenced by their reproductive condition (Chapter 4). Other yearling females that did not emigrate were seen involved in few interactions. Their social status remained unclear, but they did not appear very aggressive. It appeared that dominant squirrels were more likely to remain within the natal colony than subordinates ones, but this is highly variable depending on individual life histories, which include varying rates and types of interactions with adult residents.

Particularly among males, only dominant individuals may be able to reproduce in a high-density population (Murie and Harris 1978). Subordinate ones may be less motivated to attempt to stay in the face of aggressive behavior from adult residents, because even if they succeeded they might still be prevented from reproducing by more dominant animals

(Slade and Balph 1974). Among ground-dwelling sciurids, males almost universally disperse farther and in a greater proportion than females (Armitage and Downhower 1974; Slade and Balph 1974; Dunford 1977a; Michener and Michener 1977; Dobson 1979; Schmutz *et al.* 1980; Sherman 1979; Boag and Murie 1981b; McLean 1981). All females reproduced and therefore no essential resource appeared in limited supply. However, subordinate females may be forced to poorer sites where they and their offspring may suffer higher mortality or lower reproductive output, particularly in years of adverse weather conditions (Morton and Sherman 1978). In 1981, a severe snowstorm occurred at Dyson Creek in May, and some adult females did not produce young (W.J. King, pers. comm.).

Several studies have suggested that dispersal may be important in limiting the size of sciurid populations. It is the most important cause of loss of individuals from populations of *M. flaviventris* (Armitage and Downhower 1974), *S. armatus* (Slade and Balph 1974) and *S. tereticaudus* (Dunford 1977a), and is considered important in reducing numbers of *S. richardsonii* (Michener and Michener 1977) and *S. columbianus* (Boag and Murie 1981b). However, the role of dispersal in population regulation is unclear. Boag and Murie (1981b) suggested that populations of *S. columbianus* could be regulated through density-dependent dispersal, and Slade and Balph (1974) indicated that dispersal may be density-dependent among *S. armatus*. Among *S. richardsonii*,

where females exhibit home range inheritance, there is apparently a limit to the number of siblings that can become established whithin the mother's home range, so that some members of large litters have to take up residence elsewhere (Michener 1981). However Armitage (1975) found a high degree of variation between different *M. flaviventris* colonies in the relationship among density, dispersal and recruitment, and Dobson (1979) believed that emigration was independent of density in the populations of *S. beecheyi* he studied. During this study, a larger proportion of yearlings left the study area on the year of higher population density, so that the numbers of yearlings at the end of the two seasons were similar. Yearling emigration was the most important source of loss from the population in both years. Manipulations of density and age ratios may be necessary before the density-dependence of dispersal and its importance in population regulation can be clearly established. During this study, the spring population at Dyson Creek more than doubled from 1979 to 1980, but did not change much between 1980 and 1981. The winter 1979-80 was harsh compared with the following two (Chapter 6), and may have drastically curtailed the population below its normal levels. Within the two summers of this study, density of squirrels may have returned to its normally high level and possibly stabilized.

4. Reproduction In Yearling Females

4.1 Introduction

Among North American ground-dwelling sciurids, members of the genus *Marmota* show interspecific variation in the age at which females achieve sexual maturation. Female *M. monax* first reproduce as yearlings (Davis 1964), *M. flaviventris* as 2-year olds (Armitage and Downhower 1974) and *M. caligata* as 3-year olds (Barash 1974a). This variability has been related to food availability and length of the growing season (Barash 1974b). Among *M. flaviventris*, in which only 25% of 2-year-old females breed, successful reproduction is strongly dependent on an appropriate food supply during gestation and lactation (Andersen *et al.* 1976), also suggesting that environmental conditions may indirectly influence reproductive success by affecting the food supply.

In most species of the genus *Spermophilus*, females usually breed as yearlings, for example, *S. richardsonii* (Michener 1979), *S. parryii* (Carl 1971), *S. armatus* (Slade and Balph 1974), *S. tereticaudus* (Dunford 1977a), and *S. beldingi* (Morton and Gallup 1975). However, female Columbian ground squirrels (*S. columbianus*) in southwestern Alberta (elevation 1470 m) do not normally breed until they are 2 years old (Murie and Harris 1978); none of 866 yearling females trapped between 1973 and 1979 showed signs of sexual maturity or pregnancy (D.A.Boag and J.O.Murie, unpublished

data), and 31 reproductive tracts of yearling females revealed neither corpora lutea nor placental scars (Murie *et al.* 1980). However, Shaw (1924) stated, without presenting any data, that yearling females breed in Washington, where their active season begins about 2 months earlier.

Here I report breeding by yearling females of this species in southwestern Alberta and discuss some of the possible causes and implications of this unusual event.

4.2 Methods

The age of yearling females considered in this chapter was known with certainty, as they had been trapped as juveniles upon their first emergence in 1979.

Growth rates were calculated by dividing the change of weight in grams by the number of days over which it had occurred. Growth rates were not calculated if squirrels were captured only once, or less than 20 days elapsed between the first and the last capture.

4.3 Results

Density of the emergent (adults and yearlings) population was 31.1 squirrels per hectare in 1979 and 70.3 squirrels per hectare in 1980 (Table 1).

Emergence weight of yearling females that bred in 1980 (mean = 355g, SD = 36.1) was not significantly higher than that of nonbreeders (mean = 288g, SD = 34.3), but was

significantly higher (P = 0.01, Mann-Whitney U test) than that of nine nonbreeding yearlings trapped in the same year at Gorge Creek (mean = 246g, SD = 53.4) (J.O. Murie, pers. comm.).

In 1979 there was no significant difference between the juvenile female growth rates of those that bred and did not breed in 1980; but as yearlings in 1980, nonbreeding individuals had a greater rate of weight gain than breeding individuals during the period from emergence to weaning (July 4) (Table 7); rate of weight gain of breeding yearlings increased after weaning. Breeding yearlings exhibited a pattern of weight gain similar to adult females, that grew by 1.05 g/day from emergence to July 4 and by 3.86 g/day from July 4 to immergence.

The social behavior of yearling females that bred was different from that of those that did not, and resembled the behavior of adult females (Table 8). Yearling females that bred played less than nonbreeding individuals, both before and after May 15. After May 15, breeding yearlings were much more aggressive, both towards other yearlings (of both sexes) and towards adult females.

Of the four yearling females that bred, two established a home range in part of their mother's home range of the previous year, the remainder being held by their mother. The other two established themselves on previously unused areas that were adjacent to the home range used by their mother in both years. A similar behavior is shown by *S. richardsonii*

Table 7. Mean growth rate in grams per day (SE, N) of juvenile female Columbian ground squirrels born at Dyson Creek in 1979, and their weight gain as yearlings in 1980.

	Juveniles 1979	Yearlings 1980	
		Emergence July 4[a]	July 4 immergence
Bred 1980	8.16 (0.91, 3)[b]	2.71 (0.21, 4)	3.65 (0.73, 4)
Nonbreeders 1980[c]	7.77 (0.39, 7)	4.12 (0.20, 7)	3.15 (1.85, 2)
Difference between groups[d]	$p>0.05$	$P=0.001$	$P>0.05$

[a]July 4 chosen as weaning had occurred by then.

[b]Only three animals were caught at appropriate times to determine growth rates.

[c]Only seven animals were caught at appropriate times to determine growth rates, and only two stayed on the study area after July 4 (see Chapter 1).

[d]Mann-Whitney U test.

Table 8. Mean individual rates of playing and interacting aggressively in number per hour (SE) among breeding yearling, nonbreeding yearling, and adult female Columbian ground squirrels at Dyson Creek in 1980.

Interaction	Nonbreeding yearling (9)	p[a]	Breeding yearling (4)	Breeding adult (11)
Play with yearling				
Emergence to May 15[b]	0.211 (0.035)	<0.05	0.07 (0.031)	0
May 15 to July 10[c]	0.149 (0.048)	<0.001	0.0	0
Aggression against yearling				
Emergence to May 15	0.032 (0.014)	ns	0.047 (0.023)	0.536 (0.113)
May 15 to July 10	0.01 (0.006)	<0.025	0.098 (0.041)	0.649 (0.111)
Aggression against adult female				
Emergence to May 15	0	ns	0.029 (0.027)	0.365 (0.065)
May 15 to July 10	0	<0.005	0.043 (0.018)	0.305 (0.033)

[a]Difference between breeding and non-breeding yearling, Mann-Whitney U test.

[b]May 15 chosen as all females had been bred by then.

[c]July 10 chosen as all litters had emerged by then, see Chapter 3.

(Michener 1979), *S. tereticaudus* (Dunford 1977b), *S. beldingi* (Sherman 1980), and *S. parryii* (McLean 1981).

Average litter size of yearlings (mean = 2.75, range 2-3) was smaller than that of adult females (mean = 3.64, range 1-5). This difference, however, is not significant, possibly because of small sample size.

4.4 Discussion

Very high densities in small mammal populations are often correlated with reduced reproductive rates (Krebs *et al.* 1973). This does not appear to be true for Columbian ground squirrels (Murie *et al.* 1980); the density at Dyson Creek, particularly in 1980, was several times higher than previously reported for this species (Balfour 1979; Boag and Murie 1981b). At Gorge Creek, where densities of non-juvenile squirrels have ranged from 11.6 to 16.1 per hectare (Boag and Murie 1981b), mean litter size was 2.7 (Murie *et al.* 1980). At Dyson Creek, all adult females reproduced and mean litter size was 4.1 in 1979 and 3.64 in 1980. The combination of high density and high reproductive performance suggests that the habitat may be of particularly good quality, a situation similar to that reported by Slade and Balph (1974) for *S. armatus* on a mowed lawn. This suggestion is also supported by the high growth rate among juveniles in 1979. The average growth rate for 1155 juvenile females, trapped between 1973 and 1979 by Boag and Murie

(1981a), ranged from 3.8 to 5.5 g/day, depending on the year and was 5.4 g/day in 1979. At Dyson Creek, this rate was 7.9 g/day in 1979. Boag and Murie also noted that variations in annual growth rate appeared to be inversely correlated with total precipitation during August. Columbian ground squirrels stay underground when weather conditions are adverse (rain, heavy snow, hard frost); a prolonged period of such weather produces a drop in weight, similar to that reported for *S. beldingi* (Morton and Sherman 1978). For example, over a 6-day period of rain and snow in late May 1980, 17 squirrels decreased from a mean weight of 505g to a mean weight of 483g ($P<0.025$, Wilcoxon matched-pair test), at a time when their weight would normally be increasing. It is therefore reasonable to suspect that dry and warm conditions are necessary for maximum rates of fat storage. Such conditions prevailed in July and August of 1979, a year in which Boag and Murie (1981a) reported a very high growth rate for juveniles at Gorge Creek: only 1 rainy and cold day during these 2 months. These favorable conditions apparently allowed squirrels to enter hibernation with very good energy reserves. An exceptionally warm dry May in 1980 (average maximum and minimum temperatures were +18.6 C and +3.4 C, compared with a 6-year average at Gorge Creek of +14.7 C and -2.3 C) may have contributed to precocial maturation of these four females and allowed access to an adequate food supply, necessary during gestation and lactation in *M. flaviventris* (Andersen *et al.* 1976) and presumably in *S.*

columbianus as well.

Breeding yearling females were more aggressive than nonbreeding individuals. This suggests that aggressiveness is related to production of young (Chapter 5). However, the aggressiveness of breeding yearling females was less than that of adult females, all of which bred. This difference is in part due to the fact that two yearling females established themselves on peripheral areas seldom used by other squirrels, but it may also indicate that, although some yearlings achieved sexual development, they did not completely develop the behavioral phenotype characteristic of adult females.

Among the members of the genus *Spermophilus*, *S. columbianus* is found in habitats with some of the shortest growing seasons and highest risks of unseasonally bad weather conditions. These squirrels seem to have adapted to this environment by delaying sexual maturation, producing small litters and achieving a relatively large body size. The results of this study suggest that some of these characteristics are directly influenced by environmental conditions, and these squirrels retain the potential to exploit unusually favorable years by increasing their reproductive output through maturing younger.

5. Territoriality In Adult Females

5.1 Introduction

Adult males of several species of ground-dwelling sciurids show some form of territorial behavior (Carl 1971; Armitage 1974; Owings *et al.*1977: Murie and Harris 1978). Most often, this involves defense of and/or dominance within a territory, from which the resident tries to exclude other males, apparently to ensure access to estrous females; aggression among males is often highest during the breeding season (Murie and Harris 1978; Michener 1979).

Among females, however, spacing usually involves fidelity to a burrow system and reciprocal avoidance rather than aggression (Carl 1971; Barash 1974a; Michener 1979). Sherman (1980) reported female territoriality in *Spermophilus beldingi*, and Slade and Balph (1974) found that females became aggressive and territorial following breeding in a high-density population of *S. armatus*.

Available information on female Columbian ground squirrels (*S. columbianus*), although limited, indicates intolerance of other females near the nest burrow during lactation (Betts 1973); Kivett (1975) stated that at this time a small territory is defended around the nest burrow. Some form of spacing behavior is implied in the regulation of population size (Boag and Murie 1981b).

I studied a high-density population of these squirrels during the spring-summer of 1979 and 1980; here I describe use of space and social interactions among the adult females, emphasizing temporal changes in the location and rate of aggressive interactions throughout the season.

5.2 Methods

Behavioral observations were conducted in SA following the procedures outlined in the general methods section.

Contours of home ranges were drawn by joining all outermost sightings to form a polygon with no acute angles, unless this involved drawing a side longer than 25 meters without intersecting additional sightings. Single sightings located at 10 m or more from any other sighting or from any side of the home range polygon were not included.

Overlap was calculated as the area within a given home range shared with contiguous home ranges.

In this chapter, preweaned juveniles in the burrows are referred to as infants.

5.3 Results

The Population

The size of the population on the study area changed between years (Table 9). Spring density of adults and yearlings rose from 31.1 squirrels/ha in 1979 to 70.3 squirrels/ha in 1980. These densities are much higher than

Table 9. Columbian ground squirrels that emerged at the Dyson Creek study area (SA only) in 1979 and 1980.

		1979	1980
Adults	males	2	4
	females	10	13
Yearlings	males	5	21
	females	6	13
Subtotal		23	51
Juveniles[a]	males	26	26
	females	15	24
Subtotal[a]		41	51[b]
Grand total		64	101

[a] Includes offspring of one female each year that moved to SSD to give birth.

[b] Includes one juvenile of unknown sex.

those previously reported for *S. columbianus* (Balfour 1979; Betts 1973; Murie *et al.* 1980; Boag and Murie 1981b). Juvenile production was also higher than that of squirrels from nearby areas of similar elevation and environmental conditions (Murie *et al.* 1980). Mean litter size of adult females was 4.1 (range 3-6) in 1979 and 3.6 (range 1-5) in 1980. The mean litter size in 1980 of the eight females that had young also in 1979 was 4.1 (range 3-5). Some yearling females bred in 1980 (Chapter 4).

Most adults and yearlings emerged between 26 April and 6 May 1979 and between 20 April and 1 May 1980. Juveniles emerged between 21 June and 1 July 1979 (although one late litter did not emerge until 14 July) and between 14 and 24 June 1980 (again with a late litter on 8 July). Several yearlings of both sexes (54% in 1979 and 70% in 1980) disappeared between mid-June and early July, and are thought to have emigrated (Chapter 3). Females entered hibernation between 29 July and 13 August in both years.

Use of Space

Adult females occupied small home ranges, that rarely exceeded 1000 sq. m. Each female was sighted an average of 49 times (SD = 18.9) per Period in 1979 and 33 times (SD = 12.2) in 1980. In 1979 most of the study area was covered with snow when the first squirrels emerged, and activity was restricted to elevated, snow-free areas. Most females moved a considerable distance before settling in their home ranges: mean distance between the center of activity of the

first Period following emergence and that of Period 7 was 24.6 meters (range 5.7-40.4). In 1980, all areas were snow-free at emergence, and females tended to establish near the burrow from which they emerged, changing the location of their center of activity by an average of only 9.2 meters (range 2.3-18.4) between the first Period and Period 7. A comparison of the distance moved by eight females that stayed on SA in both years showed a significant decrease in 1980 (Wilcoxon matched-pair test, $P<0.05$). Seven of nine females surviving through the winter 1979-1980 stayed within the same home ranges in both years (mean interyear distance between centers of activity during Period 7 was 9.7 meters, range 1.1-18.6).

Overlap between home ranges was high following emergence, decreasing to a minimum during late gestation (Period 4) and then increasing again after parturition (Fig. 7). Home range size followed a similar pattern (Fig. 8). This pattern is shown graphically for eight home ranges in 1979 in Fig. 9. The increased density of adult females in 1980 was correlated with a decrease of mean home range size from 620 sq. m to 451 sq. m ($P<0.01$, Wilcoxon matched-pair test comparing mean home range size for each of the 12 Periods), but percentage overlap was almost identical ($P>0.30$) (Fig. 7).

Territorial behavior

The most common aggressive interactions were chases and fights. Those classified as 'chases' occurred over distances

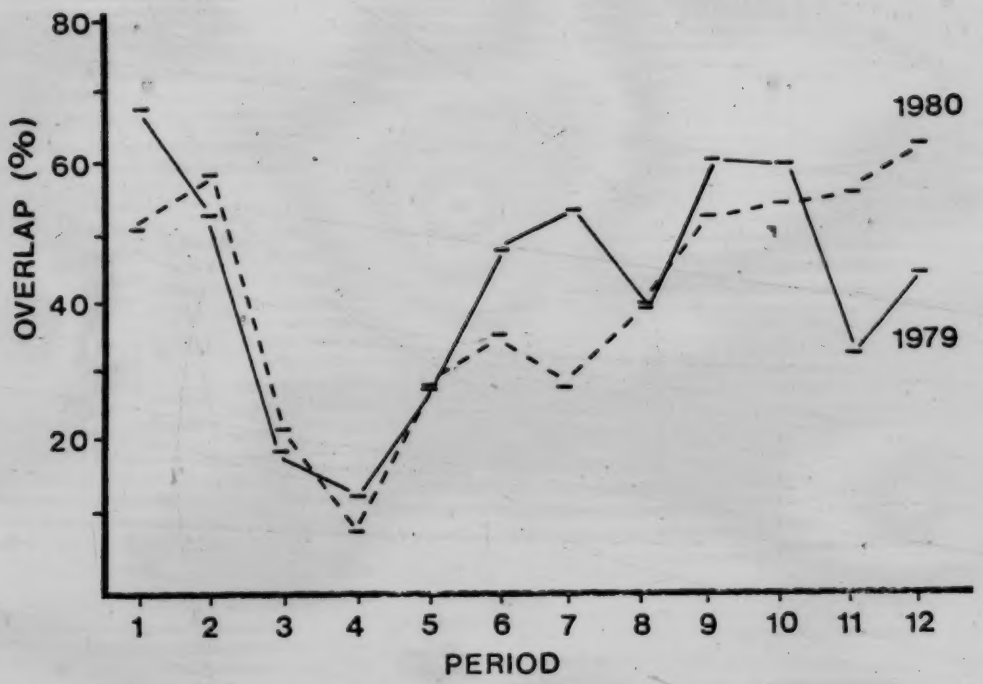


Fig. 7. Percentage overlap of home ranges of adult female Columbian ground squirrels at Dyson Creek in 1979 (N = 9) and 1980 (N = 11).

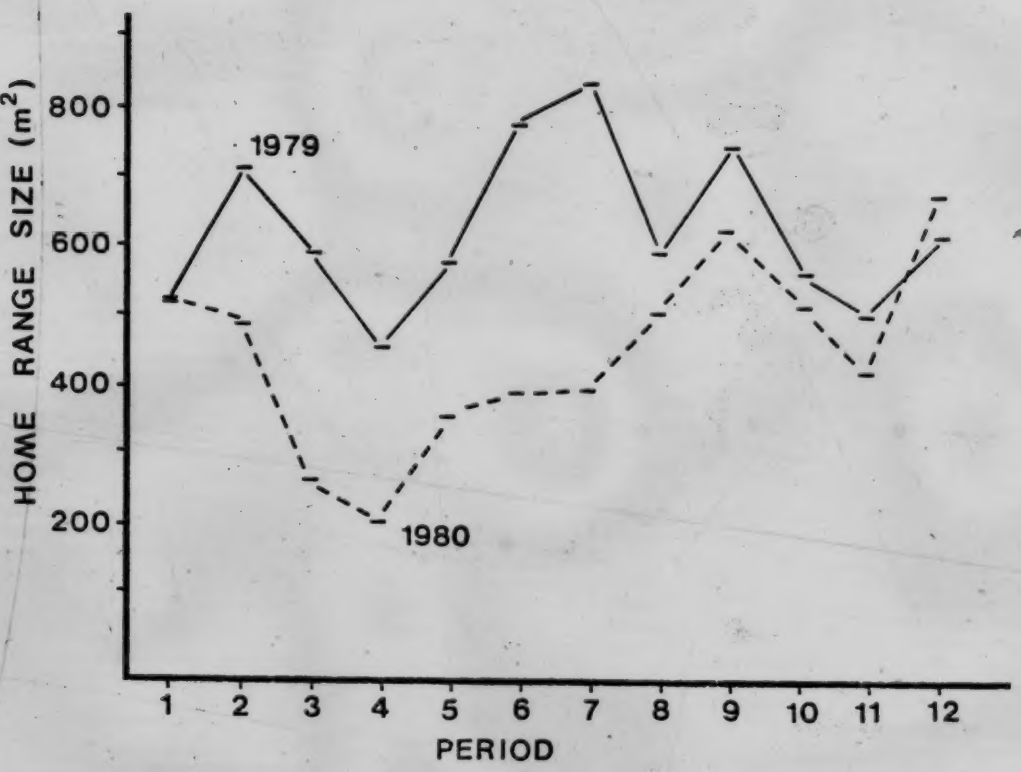
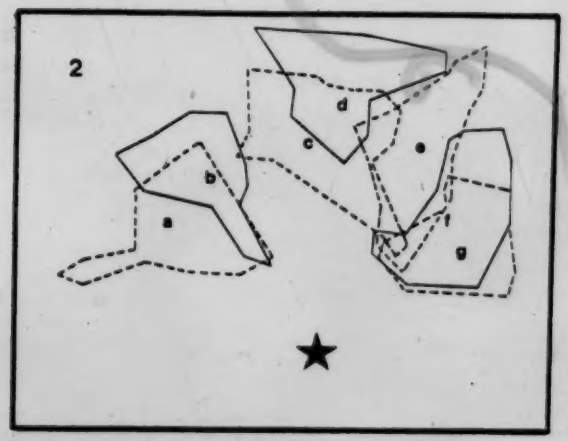


Fig. 8. Mean home range size of adult female Columbian ground squirrels at Dyson Creek in 1979 (N = 9) and 1980 (N = 11).

Fig. 9. Home ranges of adult female Columbian ground squirrels at Dyson Creek in Periods 2, 4, and 7 of 1979. Only eight are shown because one female moved to SSD and a second one did not emerge until the middle of Period 2 and did not settle in a recognizeable home range until Period 7. Each letter indicates the location of the center of activity for each Period. The star indicates the location of the observation stand (see Fig. 1).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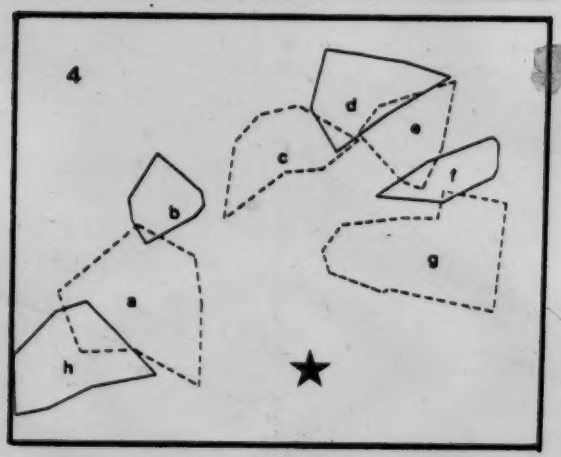
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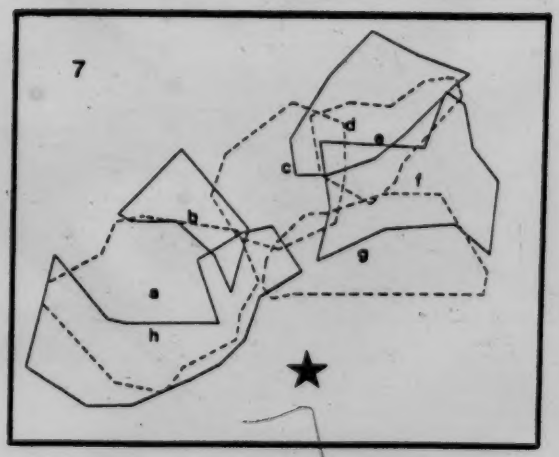
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of up to 30 m. Most ended with the chaser stopping after some distance, but occasionally turned into fights, either with the chaser catching up to the chasee or with the chasee turning on the chaser. Ball fights (Murie and Harris 1978) appeared milder than those seen between males, and usually lasted less than 3 seconds. Chase reversals often occurred, particularly during Periods 5 to 8. Up to five chase reversals may occur sequentially, sometimes each chase being 1 m or less.

Location and outcome of aggressive interactions were related to the spacing pattern described above. Each female appeared to defend the central part of her home range (a territory), within which she was dominant to other females and from which she tried to exclude them. The location of each female's territory could be determined by the outcome of her aggressive interactions. In particular, chase reversals, which occurred consistently at given locations, were interpreted as occurring at territorial boundaries (Fig. 10). The outcome of interactions in the overlap zone was predictable when based on their location relative to the boundary.

The rate of aggressive interactions followed a pattern similar to that of home range size and degree of overlap (Fig. 11). It was low in the first 2-3 days following emergence, but soon increased after breeding. Each female seemed to become suddenly aggressive at this time, suggesting that hormonal changes correlated with breeding

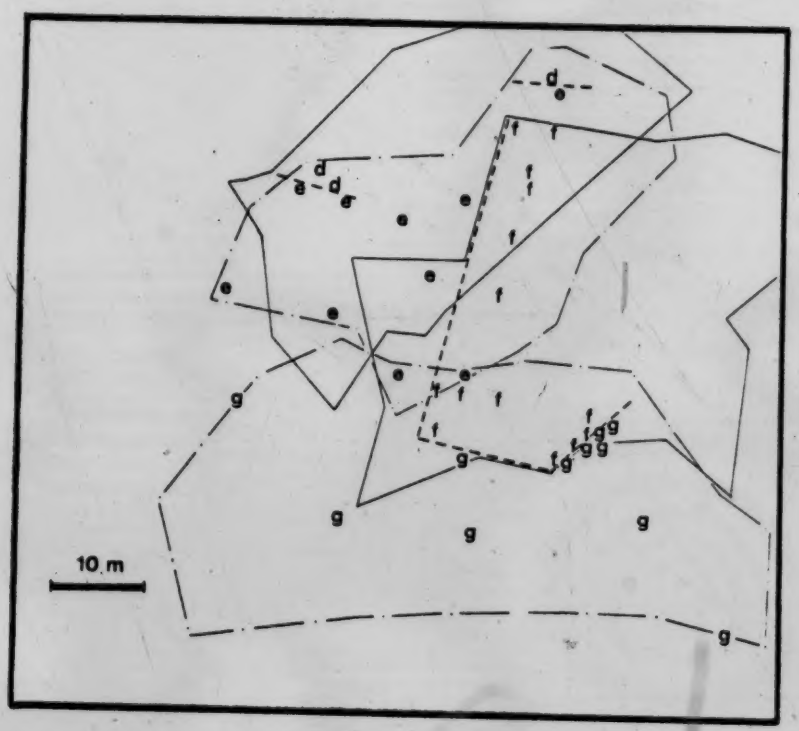

Fig. 10. Location and outcome of aggressive interactions between 4 adult female Columbian ground squirrels at Dyson Creek during Periods 5, 6 and 7 in 1979. Letters refer to the same females of Fig. 9, and indicate location and winner of an interaction. Broken lines indicate the approximate location of territorial boundaries. Solid lines and solid lines with dots indicate the contours of the home ranges used over the entire 24-day period.

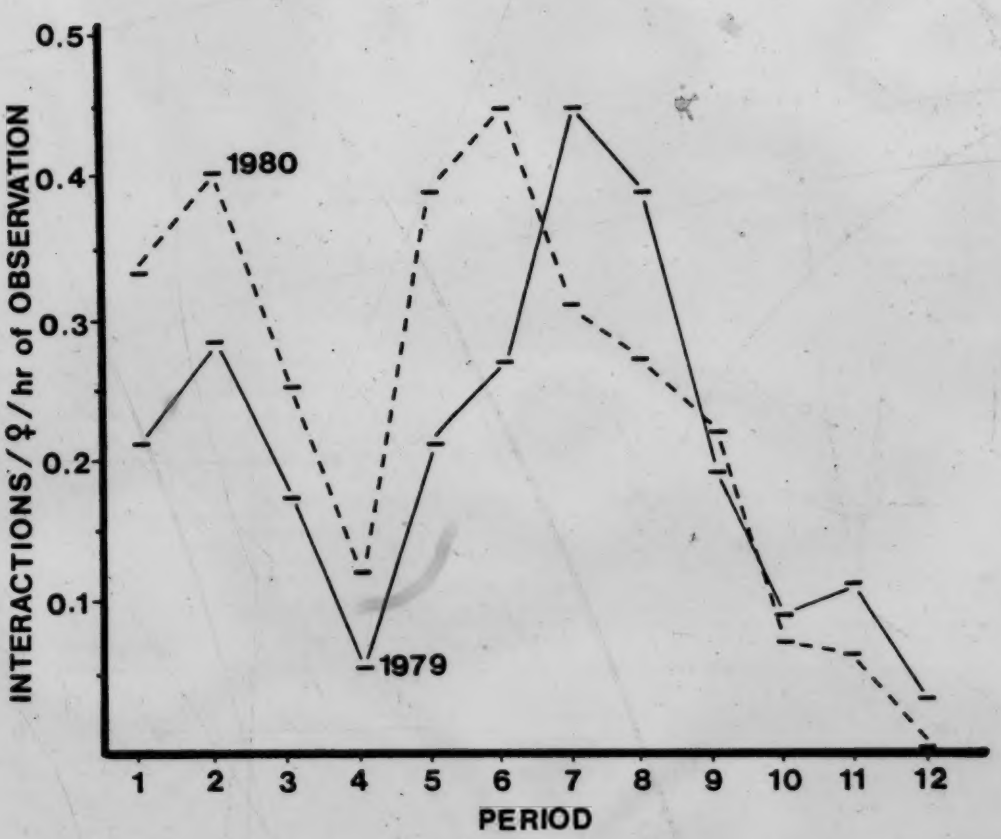

Fig. 11. Mean individual rate of aggressive interactions between adult female Columbian ground squirrels at Dyson Creek in 1979 (N = 9) and 1980 (N = 11).

may be involved. Aggressive interactions decreased near the time of parturition (Period 4), then increased again and remained common until a few days after juveniles emerged from the natal burrows. During this time, chase reversals were very common. Females were much more tolerant of each other after juveniles had emerged. Up to that time (Periods 5-6), percentage overlap was closely correlated with rate of aggressive interactions, as one would expect if these resulted from residents chasing intruders from their territory. During the 2 weeks preceeding hibernation, females were occasionally seen feeding within 0.5 m of each other without apparent interference. However, most of these observations occurred when females were outside the areas they formerly defended.

Individual rates of aggressive interactions were higher in 1980 for the first part of the season (Fig. 11), possibly reflecting a higher density of territorial females and therefore a higher probability of encounters. However, when the whole season is considered, this difference was not statistically significant (Wilcoxon matched-pair test, $P>0.25$).

Frequency of scent-marking (Kivett 1975) followed a pattern similar to that of aggressiveness (Table 10), being more common during lactation and immediately following emergence of juveniles than at any other time.

Table 10. Frequency of scent marking behavior (marks/female/10 hours of observation) of adult female Columbian ground squirrels at Dyson Creek in 1979 and 1980.

	1979			1980		
Periods[a]	# Markings	# Female-hours	Marking frequency	# Markings	# Female-hours	Marking frequency
5-8	55	755	0.73	39	567	0.69
1-4 and 9-12	31	1413	0.22	27	1233	0.22

[a]Difference between rates of marking during Periods 5 through 8 and all other periods combined. (χ^2 = 32.15 in 1979, χ^2 = 23.29 in 1980, df = 1, $P<0.001$ in both years).

5.4 Discussion

I believe these data indicate that adult female Columbian ground squirrels in the population studied are territorial over the period from breeding to weaning of juveniles. The territory consists of only part of the home range, and is actively defended against other adult females. Each female is dominant within her territory, but exclusive use is not achieved. Neighboring females will often enter a territory, and will be excluded from it only when the resident detects them. A similar spacing system is found among males of the same species (Murie and Harris 1978), while dominance, in the form of decreased submission, characterizes core areas of adult female *S. richardsonii* (Michener 1979).

Scent-marking appears to be related to territoriality, being most frequent while territories are most actively defended. It may function as a form of territorial advertisement, or it may increase the resident's confidence of being within her area of dominance (Owen-Smith 1977). Scent marking is most common among males during the breeding season when male territoriality is most evident (Kivett 1975), and an increase in its frequency associated with lactation among females was noticed by both Betts (1976) and Kivett (1975).

Previous studies have revealed the existence of territoriality among females of the genus *Spermophilus* under conditions of high density (Slade and Balph 1974). Betts

(1976) noted intolerance through chasing of other adult females near the nest burrow, and even chase reversals. His study population was dense (31 squirrels/ha) compared to the populations studied by Murie *et al.*(1980), where female territoriality was not obvious and seldom used areas existed between the home ranges of many females (J.O. Murie pers. comm.). These studies indicate that high density may be a stimulus to territorial behavior, as suggested by Whitham (1979); defense of a resource becomes advantageous only when that resource is in short supply. When the resource is abundant, territoriality may be superfluous and involve an unneccessary expenditure of energy (Betts 1973).

Murie and Harris (1978) suggested that estrous females were the "resource" defended by territorial males. It seems unlikely that access to preferred mates was the reason for territoriality in the females: only two breeding males were present in the Dyson Creek study area, and each roamed over half of it, apparently independently of the behavior of females. In addition, aggression among females did not decrease following breeding, as occurs among males.

Food was probably not involved in stimulating territoriality. Andersen *et al.* (1976) found in *M. flaviventris* a correlation between the number of young produced by a female and the amount of food available to her, and Slade and Balph (1974) listed food quality as a reason for competition for territories in *S. armatus*. However, the population at Dyson Creek was not faced by any

evident food shortage: growth rates and weights were higher than those from nearby populations (cf. Boag and Murie 1981a, Chapter 4 and Appendix 1), indicating an adequate food supply. Females raised larger litters and were also less aggressive after weaning, when most accumulation of fat for hibernation occurs (Boag and Murie 1981a).

Territoriality in *S. parryii* may be partly related to the defense of suitable hibernacula (Carl 1971). This may be an important factor in determining overwinter survival. If hibernacula played a major role in territoriality for *S. columbianus*, however, one would expect this behavior to be most evident near the time of hibernation, whereas at that time it is almost non-existent. The pattern of aggressive behavior suggests that the function of territoriality is to defend the infants. An increase in female aggressiveness during lactation has been reported in *M. caligata* (Barash 1974a), *M. olympus* (Barash 1974b), *S. richardsonii* (Michener 1979), *S. armatus* (Slade and Balph 1974), *S. beldingi* (Sherman 1980) and *S. tereticaudus* (Dunford 1977b). This suggests that protection of infants from potential predators or aggression by conspecific is involved. However, no intraspecific aggression on infants was observed, and the high litter size at emergence suggests that no killings had taken place in the burrows. Sherman (1981a) quoted Steiner (1970b, 1972) and McLean (1979) as reporting infanticide among *S. columbianus*. Neither of Steiner's papers makes specific reference to any killing and McLean (1979) does not

mention this species. McLean (1978) did suggest that plugging of nest burrows by adult females of this species following parturition may be related to protection of infants from intraspecific predation. Killing of juveniles by adult male *S. parryii* is apparently a common event, and may be related to male territoriality in that species (McLean 1981). However, only among *S. beldingi* are adult females known to kill other female's young: this occurs when a female loses her litter to a predator, and she then moves to a new area where she settles after killing the offspring of a resident (Sherman 1980). Thus, it may be that the territorial behavior shown by female *S. columbianus* is related to possible attacks by 'stranger' females (new immigrants to the colony seemed to be subject to much more frequent attacks than residents) or by residents that had lost their litter. No cases of litters being lost before emergence occurred during this study, and no evidence was obtained that lactating resident females tried to harm other female's offspring. Trespassing usually occurred during feeding, and fights were not as intense as those observed among males, as was noted by Betts (1976). This suggests that resident females were not strongly motivated to enter each other's territories. Alternatively, females may be spacing themselves out to obtain protection from predation. Although predators (primarily avian: *Accipiter cooperi*, *A. gentilis*, *Buteo jamaicensis*, *B. swainsonii*, *Falco mexicanus*; but also terrestrial: *Canis latrans*, *Mustela frenata*) were

seen to make 40 attacks during this study, only 2 juvenile squirrels were seen taken (both by *A. gentilis*). Possibly, the dispersed distribution of the squirrels made undetected attacks more difficult and thereby provided protection.

More data are required on relative survival rates of squirrels at different locations within the colony, as well as experimental manipulations, involving removal of litters and possibly introduction of females from outside the colony, before the main function of female territorial behavior is clearly elucidated.

6. Dominance Relationships Among Adult Females

6.1 Introduction

The literature on dominance relationships among males, particularly mammals (for example Geist 1971; Eisenberg *et al.* 1972; Le Boeuf 1974; Murie and Harris 1978) and polygynous birds (Wiley 1973, 1978), suggests that it is often associated with conspicuous displays and agonistic behavior. In most species, the advantage of being dominant is priority in access to resources, particularly estrous females in those studied.

Females of many species less frequently display overt agonistic behavior, and therefore any dominance relationships that may exist are more difficult to recognize. Nevertheless, their existence has been demonstrated in several species, where dominance is an important determinant of survival and reproductive success. For example, among herbivorous lizards dominant females have prior access to habitat where escape from predators is facilitated (Carothers 1981). Dominant female elephant seals (*Mirorunga angustrirostris*) experience higher weaning success and have access to optimal parturition sites; they mate with dominant males and can even directly and negatively affect the reproductive success of subordinates (Reiter *et al.* 1981).

Among ground squirrels of the genus *Spermophilus*, some females (possibly dominant individuals) appear to have access to optimal sites of residence: for example in a population of *S. parryii*, some squirrels were reported to be forced to areas where overwinter survival was very unlikely (Carl 1971), and in one population of *S. armatus*, females showed preference for mowed lawn habitat from which some of them (presumably subordinates) were excluded (Slade and Balph 1974). These studies, however, did not present any data on outcomes of aggressive interactions between individual females, nor did they try to relate dominance status to access to optimal habitat or to differential reproductive success. Murie and Harris (1978) suggested that dominance status was related to reproductive success for male *S. columbianus*, and O'Shea (1976) used agonistic interactions to construct a linear dominance hierarchy for both sexes of the African ground squirrel, *Xerus rutilus*.

Boag and Murie (1981b) speculated that social behavior was involved in excluding subordinate squirrels from high-density clumps of *S. columbianus*, which may have been located in optimal habitat. They suggested that subordinates may be forced to suboptimal habitat where they experience lower survival and reduced reproductive success. Territorial behavior, displayed by adult females of this species under high population density (Chapter 5) may be involved in this process.

Here I present data on dominance relationships among adult females of the Dyson Creek population, with emphasis on the effects of social status on access to optimal territorial sites and on the reproductive success of individual females.

6.2 Methods

Data presented here were collected according to the procedures outlined in the general methods section.

Throughout this chapter, I refer to the group of adult females with territories located on and around the main ridge in the center of SA (Figs. 1 and 9) as the "On" females. Females with territories not located on the ridge are referred to as "Off" females. Dominance relationships within groups could not be clearly determined, because dominance status changed with the location of each squirrel respective to her territory (Chapter 5). Thus, only interactions that occurred between females belonging to different groups are considered in this chapter.

Expected numbers of interactions won and lost, based on the assumption that they were random, were calculated by dividing the total number of interactions for which an outcome could be determined by the number of squirrels involved. For example, if 100 interactions (each involving 2 squirrels, giving a total of 200 individual outcomes of either a win or a loss) were seen among 10 squirrels, one

would expect that each would have won 10 and lost 10.

6.3 Results

The elevated ridge in the middle of SA (Fig. 1) differed from the rest of the meadow in several physical characteristics that appeared important to the squirrels. In 1979 most of the study area was snow-covered or flooded by runoff when the squirrels emerged (Fig. 12), but the south-facing ridge was already relatively dry. Similarly, after every snowfall this ridge was the first area to be snow-free, and it was never flooded by heavy rains, as were some areas near the creek.

The ridge also offered a good view over the rest of the meadow, a possible aid in territorial defense and in facilitating detection of approaching predators. Females often first noted intruders from a vantage point, from which they would run to encounter and chase them off their territory (Chapter 5).

In 1979, squirrels emerged only from areas that were the first to become snow-free, as determined by direct observation and observation of tracks in snow. Most squirrels appeared to emerge on the ridge, the steep hillside above the road or the far southern corner of the meadow, also an elevated area (Figs. 1 and 12). In 1980 and 1981, the meadow was snow-free when the squirrels emerged. Twenty-one were already active on 24 April 1980 and 6 on 17

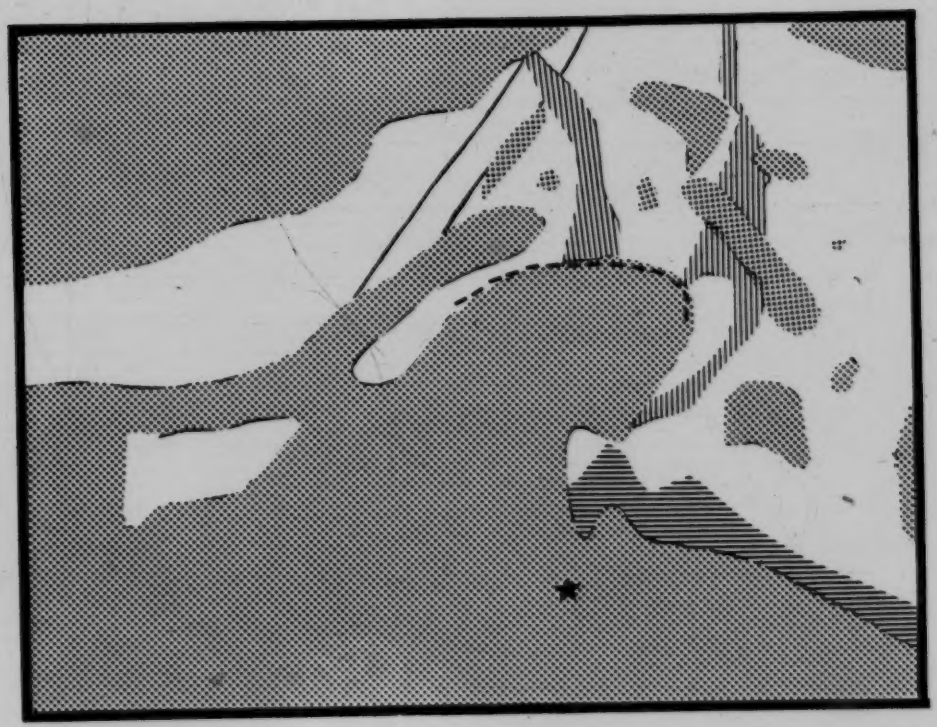

Fig. 12. Snow cover at the Dyson Creek study area on 26 April, 1979. Shaded areas were covered by either snow or ice, and vertical striping indicates runoff water. Dyson Creek was mostly frozen, the rest is indicated by horizontal striping. The star indicates the position at which the observation stand was located from mid-June. Roads were mostly covered with snow, except for the short section outlined in this map. The broken line outlines the top of the ridge.

April 1981, when I made the first visits to the study area. Location of burrows used by squirrels as hibernacula could not be determined as accurately as in 1979, but apparently most emerged from elevated areas, mainly the ridge.

The lower flat areas near the creek, completely covered by snow in late April 1979 (Figs. 1 and 12), were not used by any squirrel that year until after the breeding season (mid-May). Throughout this study, this area appeared to be less preferred by adult females. Most avoided it until after emergence of juveniles, when they moved more widely outside their territories (Chapter 5).

"On" females appeared to be dominant over "Off" females (Table 11). They won most interactions, particularly in 1979. In 1980, a 2-year old female (the only non-disperser of a group of yearlings that frequented the ridge in 1979, see Chapter 3) established a territory on the ridge. Possibly because of her younger age (Murie and Harris 1978; Pack *et al.* 1967), this squirrel lost 12 and won only 6 interactions against "Off" females. Nine of these interactions were lost to a single adult "Off" female. If this 2-year old is excluded, then "On" females won 26 and lost 13 interactions with "Off" females in 1980 (chi-square = 23.59, $P<0.005$).

Of the 9 adult females that set up territories on SA in both 1979 and 1980, only 2, which ultimately established on the flats near the creek, significantly changed the location of their home ranges. One moved to SSD. The behavior of the

Table 11. Outcome of aggressive interactions between adult female Columbian ground squirrels inhabiting the ridge area of Dyson Creek (On) and other adult females of the same colony (Off).

Year	Outcome	N	%	p^a
1979[b]	On win	61	64.2	<0.001
	Off win	20	21.1	
	Unclear	14	14.7	
1980[c]	On win	32	50.8	>0.1[d]
	Off win	25	39.7	
	Unclear	6	9.5	

[a] Based on $/^2$ comparing numbers won by On and Off. See text for calculation of expected frequencies

[b] Four On females and six Off females

[c] Five On females and nine Off females

[d] Only data from the six Off females that reared young were included in the test. The three that disappeared before their young emerged lost four and won no interactions with On females.

second is notewhorthy; she first tried to establish on a neighboring territory (defended by another "Off" female), being often seen carrying nest material to a burrow located inside this territory. The resident female, however, chased her every time she saw her. Eventually, the intruding female ceased her incursions and set up a territory in unoccupied space on the flat, but at some distance from the location of her previous year's territory; in 1980 her juveniles emerged from a burrow 24 m away from that used in 1979. This contrasts with six other adult females that had young in both years of this study. They moved their juvenile emergence burrow (nest burrow?) by an average of only 10.6 m (range 4-18). The only other female that had a territory on the flat in 1979 moved an even longer distance (38 m), across Dyson Creek to SSD. In 1979, these two females lost 59 (88%) of the 67 agonistic interactions they had with other adult females.

"On" females had larger litters in both years, and their offspring enjoyed better survival (Table 12). This was particularly evident in 1980, when juvenile survival over the summer was lower than in 1979 (chi-square = 6.65, $P<0.01$). Considering only those juveniles that survived to hibernation, in 1980-81 significantly more of those born to "On" females than "Off" females survived their first winter (chi-square = 4.25, $P<0.05$).

Average weight at emergence was higher (447 vs 407 g in 1979, and 502 vs 446 g in 1980), although not significantly,

Table 12. Production of juveniles by two groups of adult female Columbian ground squirrels at the Dyson Creek study area, and their subsequent survival.

Year	Female group	Mean litter size at juvenile emergence (range)	Total juveniles produced	Surviving to hibernation			Surviving to next spring		
				N	%	*P* [a]	N	%	*P* [a]
1979	On	4.5 (3-6)	18	17	94.4	>0.5	17	94.4	>0.1
	Off	3.8 (3-6)	23[b]	20	90.9		19	86.4	
1980	On	4.2 (3-5)	21	17	81.0	>0.1	16	76.2	<0.025
	Off	3.2 (1-5)	19	11	57.9		7	36.8	

[a]Comparison of survival rates between the two groups of females based on χ^2

[b]One juvenile from this group was collected and not included in calculating % survival.

for "On" females than for "Off" females (Mann-Whitney U test).

Overwinter survival of adult females was high in both years: only one "Off" female disappeared overwinter in 1979-80, and all adult females survived the winter 1980-81. No adult females disappeared over the 1979 active season, while 3 "Off" females disappeared in 1980. Of these, one 2-year old was unaccounted for and probably died, another had a large wound infested with maggots and was killed (she could not move when last caught by hand), and one adult became ill (she could barely move and was easily caught by hand), disappeared in mid-lactation, and presumably died.

6.4 Discussion

Adult females in this population display territorial behavior, each being dominant within its territory to all others during gestation and lactation (Chapter 5). Therefore it is difficult to separate absolute dominance from site-dependent dominance. Some interactions do occur before territories are set up, at which time absolute dominance may be established, with dominant females having access to the best sites. However, territories seem to be well-established immediately after breeding, generally within 5 days of emergence (Chapter 5). Possibly, a few aggressive interactions are sufficient to establish dominance relationships, and these may have gone largely unnoticed.

Since several females emerged (or were first sighted) in 1980 within the territories they held in 1979, their status was possibly determined by interactions that took place the previous year. Evidence suggested that territorial sites differed in quality, hence some may have been preferred over others. Thus, adult females occupying preferred territories may have won more interactions with females established elsewhere because the latter frequently intruded onto preferred sites where they lost interactions because they were outside their area of dominance. Females established on apparently optimal sites were likely to be less motivated to enter other female territories, and hence lose fewer interactions. This is further complicated because it is likely that non-ridge territories were not all of equal quality. Thus, some "Off" females, although subordinate to "On" females, were dominant to other "Off" females. For example, the two established on the flat area near Dyson Creek in 1979 appeared to be subordinate to all others.

Age also appeared to have an effect on social status. Two-year-olds were generally subordinate to older females, and in 1980 only one of five established a territory on the ridge. The young age (2 years) of one of the five "On" females in 1980 was perhaps responsible for her losing several interactions. Exact ages of adult females first trapped in 1979 were unknown, and possibly those assumed to be subordinates were mostly younger individuals, as suggested by their slightly lower weight at emergence (Boag

and Murie 1981a). Dominance has been related to age in other sciurid species (Pack *et al.* 1967), in male *S. columbianus* (Murie and Harris 1978) and in other mammals (Eisenberg *et al.* 1972; Reiter *et al.* 1981).

Fewer interactions occurred in 1980 than in 1979 between "On" and "Off" females, although the rate of aggressive interactions among adult females was higher in 1980 (Chapter 5). Possibly, subordinates made fewer incursions into the dominant's territories in 1980 because they were less motivated to move away from non-ridge areas as early in the season the conditions there (without snow or runoff) were less harsh than in 1979.

What made some territorial sites more attractive than others? Food seemed unlikely to be involved. Although detailed vegetational analyses were not undertaken, there is no evidence that important differences in food resources existed between territories. Dominant females were located on what appeared to be an optimal site for detecting approaching predators. This was facilitated not only by the elevated nature of the ridge, but also by the central location in the colony of their territories. Predators approaching from the edge of the colony would likely have been detected by peripheral squirrels, that were also in the greatest danger of being caught because they were the first to be met by the predator (Coulson 1968). A similar situation occurred among those members of a *S. armatus* population that lived in a mowed lawn (Slade and Balph

1974), a central and apparently preferred habitat within the colony. Wehrell (1973) observed a small colony of *S. richardsonii* and found that the most dominant adult female occupied the center of the colony, and the most subordinate ones were located at the periphery. Peripheral females attempted to move centripetally, but were prevented from doing so by the dominant "central" females. Less predation is likely the reason for the better survival of juveniles from the ridge over the summer of 1980, although this difference is not statistically significant (Table 12). A combination of improved overwinter survival, possibly reflecting better hibernacula, and lower losses to predation appear to be the main advantages of having access to the ridge. Juveniles apparently hibernated within or near their mother's territory.

Dominance status of mothers may influence the fitness of their offspring. The only 2-year old female that established a territory on the ridge in 1980 was resident there as a non-territorial yearling in 1979, possibly the young of an "On" female in 1978. Home range inheritance by female offspring has been reported for other ground squirrels, and may occur in *S. columbianus* (Chapter 4). It is therefore likely that young females born to dominant individuals will settle on the ridge more often than those born to subordinates.

Social status did not appear to directly affect breeding; all adult females that survived to the time of

parturition produced at least some young in both years of this study (Chapter 5), furthermore, in 1980, four yearling females (subordinate to adults, see Chapter 3) also raised litters (Chapter 4). It seems that subordinate females, once they recognize their social status, cease trying to improve it and settle in available space. Such may be dictated by the energy budget available to a given female emerging from hibernation. Possibly, only a small amount of energy can be expended early in the season for social interactions, given the energy costs of reproduction (Betts 1976), and subordinates may improve their reproductive success by avoiding dominants rather than challenging them. This may be particularly true for younger females, that established territories mostly in non-ridge habitat. Slade and Balph (1974) found that reproductive success of yearling female *S. armatus* (thought to be subordinate to adults) was better in suboptimal than in optimal habitat, possibly because of lesser social stress from interactions with dominant adults. This may also explain why Boag and Murie (1981b) found no evidence of better reproductive success on those parts of their study area which were presumed to be preferred because of the greater density of squirrels thereon. At Dyson Creek, subordinates appeared to be trying to make the best of a poor situation (Wilson 1975; Whitham 1980). In fact most of them, particularly in 1979, had at least some offspring that survived to the following spring. However, it is possible that they and/or their offspring may suffer greater

mortality and poorer reproductive success in years of adverse weather conditions. Overwinter survival may be greatly affected by spring weather conditions in some years; for example, no squirrels emerged from the flat areas near Dyson Creek in the spring of 1979, but squirrels successfully hibernated there in 1979-80 and 1980-81. Possibly, when overwinter conditions are adverse, a situation similar to that found by Carl (1971) among *S. parryii* may occur, with very high mortality among subordinate squirrels.

7. Concluding discussion

Fretwell and Lucas (1970) presented a model of habitat selection in which some individuals were excluded from optimal sites by the territorial behavior of resident conspecifics. This model was later extended by Whitham (1980) who pointed out how, when social dominance and/or territoriality are present within a population, expected fitness of individuals may vary within the same habitat. The Dyson Creek population seems to fit this model, because there apparently dominant squirrels had access to what appeared to be optimal habitat. Possibly as a result of aggressive behavior from adult residents, most yearlings, subordinate to adults, left the meadow, which could be considered 'preferred habitat' when compared to the surrounding forest. Only a few yearlings remained in the meadow, and moved to sections of it which also appeared suboptimal, because of their physical attributes and because all squirrels that lived there appeared to be forced to do so by dominant residents. Within the meadow, adult females that appeared dominant had access to central sites, where they seemed to enjoy greater fitness. These sites may have contained better hibernacula, but this remains to be determined.

Subordinate squirrels adopted alternative strategies to maximize their fitness. Most yearlings apparently emigrated, presumably in search of new habitat where they may have had a better chance of reproducing. Subordinate adult females

settled in habitat that appeared less preferred, but where space was available, and succeeded in raising some young.

Boag and Murie (1981b) postulated that population regulation in *S. columbianus* was intrinsic and dependent mainly upon exclusion of subordinate squirrels from optimal habitat through aggressive behavior of dominant individuals. Data from this study support this hypothesis. At Dyson Creek, there was no evidence that food was limited, because weights and growth rates of squirrels from this population were higher than those of squirrels from nearby areas (Boag and Murie 1981a). Natality, as measured by litter size at emergence, was high and did not decrease for the same females when population density increased. In the year of greater density, even four yearling females had young. Thus, high densities did not appear to affect reproductive rates of these squirrels, in the 2 years of this study. Murie *et al.* (1980) suggested that average litter size may increase with population density. This suggests that either a positive feedback mechanism exists, or that high densities are found in habitats of superior quality that allow a greater reproductive output.

It appears that reduction of population size is mainly dependent upon emigration exceeding immigration of immature squirrels. This seems to be density-dependent and socially-induced. Population regulation could be achieved by an increased aggressiveness of adults toward yearlings when density is high; during the 2 years of this study the number

of yearlings before dispersal increased by 157%, but as most yearlings disappeared before hibernation, adults increased by only 58%. Adult females increased by only 40%. Emigration of yearlings coupled with occasional mortality of resident adults could then effectively limit population size. Social pressure against subordinate adult females may also result in an increased overwinter mortality during severe winters, if these females are in fact forced to suboptimal habitat with poor hibernacula. Predation by raptorial birds, canids and felids probably plays a minor role because it appeared to be mainly restricted to juveniles. This loss seemed unimportant in population regulation as the major density-dependent decrease occurred among yearlings. Therefore losses of juveniles could be compensated the following year by adjusting the number of yearlings that emigrate. Even if all disappearances unaccounted for and not thought to represent emigration were attributed to predation, predators would still not be very important for population processes. No non-juvenile squirrels disappeared in 1979, and only three possible losses to predation (an adult male and a 2-year-old of each sex) occurred in 1980. However, the number of juveniles that disappeared increased from 3 (7%) in 1979 to 19 (37%) in 1980. This large variation suggests that predators may be more important in some years. If all juvenile disappearances were attributed to predation, then even predation could be thought of as being dependent upon social status, because more offspring

of subordinate females disappeared than those of dominant females. Predation may be more important for those populations preyed upon by badgers (*Taxidea taxus*) (Slade and Balph 1974) which, although present in the Sheep River area, were not recorded at Dyson Creek during this study.

Because of the harsh and unpredictable environment they live in, Columbian ground squirrels are likely to experience occasional catastrophes that may be to a large degree density-independent, such as very cold and snowy springs, late summer snowstorms, floods, etc. When these occur, it is likely that the reduced density will result in lowered social stress, such that less emigration is induced and populations can rapidly build up to their original size.

When dispersing yearlings join another colony, they will likely behave in accordance with their previous experience and social status within the maternal colony. I predict that the most dominant among the dispersers will keep (or regain) their high status when entering a new colony. Given that most other colonies appear to display a lower density, dominant immigrants from a high-density population such as that at Dyson Creek will likely be more socially experienced than the residents of the colony they enter. Coupled with their larger size, this may confer on them a high social status. Therefore those (presumably few) emigrants that survive the dispersal movement and enter a new colony may enjoy high reproductive success.

Nothing is known about how *S. columbianus* colonize previously unexploited habitat. In 1981, I observed single ground squirrels at each of three isolated grassy meadows in the Sheep River area. None of these meadows was known to have been inhabited by ground squirrels during the past 5 years. I sighted one of these squirrels several times in the same meadow, from late June to August. Possibly, subordinate emigrants from high-density colonies are more likely to found new colonies than are more dominant emigrants, as the former may be less social. I suggest that new colonies are started when a dispersing yearling female of low social status settles in an uninhabited meadow, and is joined by one or more dispersing males, also of subordinate status. These hypotheses could be tested by a comparative study of several small colonies within an area. Armitage (1975, 1977) found that the degree of sociality and intraspecific aggression varied considerably between colonies of *M. flaviventris*. Similar intercolony differences among *S. columbianus* may indicate different phases of the colonization process. Continuing study of the Dyson Creek population will allow to test this hypothesis.

Another question that remains unsolved is why the squirrels at Dyson Creek appeared to be different, physically and behaviorally, from those studied in other locations (Betts 1976; Murie and Harris 1978; Murie *et al.* 1980; Boag and Murie 1981a,b; and J.O. Murie pers. comm.). Basically, these squirrels grew faster, achieved a larger

size, matured younger, were more aggressive, produced more young and experienced lower overwinter mortality. Most of those born in the meadow, however, disappeared through emigration, which exceeded immigration. These characteristics comply with the requirements of Geist's (1971) 'high-quality population' model for temperate ungulates. According to his 'dispersal theory', when Pleistocene populations of ungulates invaded new habitat in the face of retreating glaciers, they found an abundance of food that allowed development of large size, energy-costly weapons and aggressive behavior for intraspecific competition. High-quality populations can be maintained by high mortality which would keep numbers well below carrying capacity, so that the food supply is not depleted (Geist 1971). This appeared to be the case at Dyson Creek where, although mortality was low, a large proportion of animals were effectively removed from the population each year through emigration. This theory also predicts a short lifespan: this could be verified by continuing study of this population.

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9. Appendix 1: Weight Dynamics of Dyson Creek Columbian Ground Squirrels

A. Adult females

	1979			1980		
	mean	N[a]	(range)	mean	N	(range)
April	427	4	(370-487)	479	13	(340-580)
May 1-15	450	9	(350-535)	530	11	(390-700)
May 16-31	535	9	(445-642)	560	6	(475-673)
June 1-15	578	9	(505-668)	565	7	(470-653)
June 16-30	585	10	(500-681)	561	10	(485-650)
July 1-15	569	7	(495-663)	632	9	(478-655)
July 16-31	688	8	(610-760)	633	9	(532-717)
August	696	2	(625-768)	666	5	(543-780)

[a] Number of squirrels weighed during each time interval. If a squirrel was weighed more than once, the average of these weights was used in calculating the mean.

B. Adult males

	1979			1980		
	mean	N	(range)	mean	N	(range)
April	529	2	(458-600)	472	4	(280-550)
May	560	2	(505-616)	499	3	(383-625)
June	647	2	(600-695)	522	2	(585-660)
July	960	1		811	2	(795-828)

C. Yearling females

	1979			1980		
	mean	N	(range)	mean	N	(range)
April		0		310	10	(265-363)
May 1-15	223	5	(190-265)	387	10	(235-445)
May 16-31	307	6	(200-363)	434	11	(355-508)
June 1-15	404	7	(300-445)	455	12	(395-527)
June 16-30	388	3	(330-430)	500	10	(443-567)
July 1-15	476	4	(435-550)	521	6	(450-573)
July 16-31	547	4	(538-610)	576	6	(543-640)
August		0		581	4	(538-645)

D. Yearling males

	1979			1980		
	mean	N	(range)	mean	N	(range)
April	271	2	(260-283)	343	14	(283-400)
May 1-15	283	5	(200-332)	411	15	(300-305)
May 16-31	351	6	(235-443)	504	19	(420-575)
June 1-15	452	6	(293-522)	540	19	(490-590)
June 16-30	410	2	(320-500)	604	6	(540-630)
July 1-15	528	3	(396-610)	689	3	(665-713)
July 16-31		0		684	5	(555-753)
August	550	2	(480-620)	740	2	(725-755)

E. Juvenile females

	1979			1980		
	mean	N	(range)	mean	N	(range)
emergence	127	7	(105-140)	105	19	(90-130)
June	151	11	(105-215)	137	15	(90-178)
July 1-10	226	9	(135-295)	249	10	(190-313)
July 11-20	307	10	(150-395)	342	10	(275-400)
July 21-31	406	12	(230-490)	393	11	(330-455)
Aug 1-10	448	7	(345-510)		0	
Aug 11-25	427	3	(330-505)	416	6	(385-463)

F. Juvenile males

	1979			1980		
	mean	N	(range)	mean	N	(range)
emergence	126	9	(115-140)	108	19	(95-120)
June	151	22	(125-208)	149	22	(95-250)
July 1-10	243	19	(125-340)	296	9	(230-350)
July 11-20	363	18	(303-410)	365	15	(323-405)
July 21-31	432	17	(365-478)	428	12	(375-488)
Aug 1-10	483	16	(435-540)		0	
Aug 11-20	510	1		434	4	(410-450)